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GEOGRAPHIC VARIATION IN THE RED-EYED TOWHEE OF THE EASTERN UNITED STATES

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No. 5 — *Geographic Variation in the Red-eyed Towhee of the Eastern United States*[1]

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INTRODUCTION

Previous investigations of geographical variation in the species *Pipilo erythrophthalmus* have been carried out by several individuals. For the most part these workers have considered only certain segments of a species of wide distribution in North America. Ranging from the Transition and Upper Austral zones east of the Great Plains from southeastern Saskatchewan, southern Manitoba, southern Ontario and southern Maine, south to central Texas, the gulf coast and peninsular Florida, the Red-eyed Towhee is subject to a variety of environmental conditions.

As a result of these earlier works, seven names have been proposed for use in designation of geographic races within the species. The present investigation was undertaken to determine the validity of these names, to determine the validity of the five races for which the names were proposed, to delimit the ranges of those races deemed valid, to gain additional knowledge of geographical variation within the species and within the various subspecies, and to add to the present store of information concerning the migratory behavior of the several populations. It was hoped that these lines of investigation might also shed some light on the reasons for the geographical variations observed.

MATERIALS AND METHODS

As true of most early workers in ornithology the pioneers in dealing with this species were forced to rely on small samples of populations which have wide geographic ranges. In the hope that the statistical analysis of larger series might prove enlightening a total of approximately 2300 specimens was assembled from various museums and private collections. The sources of these specimens, the number of specimens examined, the abbreviation for the collection used in the body of this report, and the persons to whom I am deeply indebted for arranging the loans are listed here.

American Museum of Natural History, 538 (AMNH) through J. T. Zimmer; Chicago Natural History Museum, 158 (CNHM) through E. R. Blake; Florida State Museum, 24 (FSM) through Nile C.

Schaffer; University of Georgia, Department of Zoology, 84 (DZUG) through E. P. Odum; Louisiana State Museum, at Louisiana State University, 106 (LSU) through George Lowery; Museum of Comparative Zoology at Harvard College, 131 (MCZ) through J. L. Peters; Carnegie Museum, 114 (CM) through W. E. C. Todd; United States National Museum including the collections of the Biological Survey, 770 (USNM) through A. Wetmore and A. J. Duval; University of Michigan Museum of Zoology, 83 (UMMZ) and the Max M. Peet collection at this same institution, 45 (MMP) through J. Van Tyne; North Carolina State Museum, 7 (NCS) through F. S. Barkalow, Jr.; Department of Biology, University of Florida, 6 (DBUF); private collections of Pierce Brodkorb, 7 (PB); G. M. Sutton, 17 (GMS) and Gideon Nelson, 6 (GN). Fifty-nine specimens in the Charleston Museum (CHAM) were not available on loan and they were studied in that museum through the kindness of E. Milby Burton, Director.

My own collections (JCD) from Gainesville and vicinity were augmented by field trips to various localities. April 17, 18, and 19, 1947, were spent on Dog and St. George Islands, Franklin County, Florida. July 22–27, 1947, was spent in southern Florida, Dade, Broward, Palm Beach, Martin and Monroe Counties. April 14–17, 1949, was spent in peninsular Florida, Hillsborough, Manatee, Sarasota, Broward, Charlotte, Polk and Martin Counties. April 20, 1949, was spent near Brunswick, Glynn County, Georgia, securing topotypical material and July 7–10, 1949, was spent in a trip to Mobile, Mobile County, Alabama, and the intervening territory in the panhandle of western Florida. These efforts contributed 83 specimens which are now deposited in the collection of the Museum of Comparative Zoology at Harvard College.

The following information was recorded from the museum label: museum number, locality, collector, date of collection, iris color, and any notation which the collector may have made in regard to condition of gonads and so forth. The condition of plumage with respect to amount of wear was judged subjectively and arbitrarily noted as fresh, slightly worn, worn, or very worn. Badly frayed specimens were excluded from consideration in examining the material in connection with wing length and tail length. The number of pairs of rectrices showing white on the innermost web was recorded. Individual variations in plumage color were noted — albinism, white tipping of the secondary coverts, abnormal color pattern of the contour feathers, and so forth.

The age of male specimens was judged on the basis of difference in color between the pale unmolted primary coverts and the darker

secondaries in birds of the year. According to Dwight (1900) this difference in color does not occur in older birds. There appeared to be no difference in measurements in these two classes, and in the final analyses of data all specimens which had undergone the postjuvenal molt were utilized.

Iris color of specimens collected by other persons was for the most part lacking. When notation of color was made, in many instances it was extremely difficult to use. It is worthwhile to point out some of the specific difficulties encountered in that many of them could be avoided by proper techniques on the part of collectors in the future. Many, certainly the majority of the specimens lacked any notation as to iris color at all. A great variety of words and phrases were used to describe the color, such as straw, buff, orange, yellow tinged with red, red tinged with yellow, salmon, brownish, red brown, light, scarlet, deep red, like the flanks, same as female No. 0000 (but no such female in the material at hand), almost like the Florida bird, light red, clear yellow, white, yellowish white. These represent a sampling of some of the designations used. It is apparent that there has been a tendency on the part of collectors to record iris color if they thought that it was unusual to have a particular color in the locality from which the specimen was taken. If the color present was thought to be the usual one in that particular locality then no notation was made. This presents certain difficulties. What did the collector assume to be the normal color and on what basis? Did he single out this bird in the field and collect it because of its unusual iris? As a result it is very difficult to visualize true conditions with respect to this important geographically varying character.

Iris color on material taken personally was, in so far as possible, noted in terms of the color charts published by Maerz and Paul (1930). In addition, if it was practical to bring the birds in the flesh to the University of Florida, Miss E. Coogle, Staff Artist in the Department of Biology, recorded iris color on the label with matching water colors. At this time comparison was made with Maerz and Paul and the color match noted on the label.

Measurements were all recorded in millimeters after having been made as described below.

Wing length. Measured flat with right angle rule against bend of folded wing, and feathers pressed to fullest extent, to end of longest primary.

Tail length. Measured with dividers, one point of which was inserted between the shafts of the middle pair of rectrices at the base and pressed forward as far as it would go, the other touching the extremity of the longest rectrix.

Culmen. Measured with dividers from the base to the tip of the upper mandible.

Depth of bill. Measured with vernier calipers, one arm on highest portion of culmen, the other across the lower edge of the mandibular rami at the end of the rhamphotheca.

Width of lower mandible. Measured with vernier calipers, across the chin, at the widest point of the rhamphotheca.

Tarsus. Measured with dividers, from the tibio-tarsal joint on the outer side to the lower end.

Middle toe. Measured with dividers, from the lower end of the tarsus to the base of the claw.

Tail spot. Measured with vernier calipers, one arm at upper limit of white on inner web of outermost rectrix, the other touching the end of the feather.

Wing spot. Measured with vernier calipers, one arm at the distal end of the primary coverts, the other at the greatest extent of white on the primaries.

Depth of bill was not utilized in arriving at conclusions presented here. It appeared that the technique of measurement for this character as outlined above was not reliable. Specimens measured twice did not produce the same results within limits of what might be considered reasonable. Individual techniques as practiced by various collectors seemed to materially influence the results obtained in measuring. Wing spot was also eliminated in that no proper technique was found for producing accurate measurements of this character.

Data were recorded on standard 5 x 8 inch McBee Keysort cards. It was hoped that these cards would serve in such a study as this, but the multiplicity of characters and variation of these characters precluded their use in the manner for which they were designed.

The specimen cards were sorted into many small samples, approximately 50, representing small geographic areas, and studied as fractional parts of the whole population to better visualize general trends in variation of the separate characters. In this material were included only those birds that were felt to be definitely breeding or resident individuals. The criterion used in this regard was arbitrarily the date of collection — May through August. Undoubtedly many individual breeding specimens were thus excluded, but it was felt that any bias encountered here was on the conservative side. Winter, or non-breeding specimens were considered as being those birds taken from November through February for the northern areas, and October through April for the Florida material. September-October and March-April specimens were considered as possibly being on migration and were excluded for this reason.

At the conclusion of the collection of data standard statistical methods of analysis were used as outlined by Simpson and Roe (1939, 1942), and Cazier and Bacon (1949).

HISTORICAL SUMMARY

Of the seven names proposed for use in dealing with the various populations of *Pipilo erythrophthalmus* Linnaeus, *Passer niger, oculis rubris,* (Catesby, 1731: 34, pl. 34) furnishes a point of departure. Catesby described the "towhee-bird" on the basis of birds seen, and presumably taken, in South Carolina. Linnaeus (1758: 180) proposed the name *Fringilla erythrophthalma* for Catesby's bird. Vieillot (1819: 292) placed it in the genus *Pipilo* which he had erected (1816: 32) and proposed a new name *Pipilo ater* for use in designating this species.

Elliot Coues (1871: 366, footnote) recognized a new form from measurements of specimens taken at Dummitts, Florida, by C. J. Maynard, and published by Allen (1871: 283). He suggested the name *Pipilo alleni* for this form.

Maynard (1878: 113, pl. 4) later proposed *Pipilo leucopis* for this same form. Shortly thereafter he (Maynard, 1881: iv) indicated that he felt that Coues had, though perhaps inadvertently, usurped a prerogative of his in taking this action.

A. H. Howell (1913: 202) proposed a fifth name, *Pipilo erythrophthalmus canaster,* for a form occurring at Spring Hill, Alabama.

H. C. Oberholser (1938: 641) stated that the birds of New Orleans and vicinity were sufficiently different from the remainder of the population to be worthy of subspecific rank and designated these birds as *Pipilo erythrophthalmus leptoleucus.*

Walter Koelz (1939: 121) proposed the seventh available name, *Pipilo alleni rileyi,* for use in designating the birds found at Brunswick, Georgia, which he felt were different from the Florida form.

Action by the American Ornithologists' Union to date (1886, 1895, 1910, 1931 and various supplements) has accorded recognition to *Pipilo erythrophthalmus erythrophthalmus* (Linn.), *Pipilo erythrophthalmus canaster* Howell and *Pipilo erythrophthalmus alleni* Coues. The type locality of *P. e. erythrophthalmus* has been designated as South Carolina by this same group.

Much attention has been paid to geographic variation in the species, and efforts were made on the part of the original describers and by others to come to conclusions as to the geographic range of the various forms. Howell (1932: 449) amended his original statements in connection with *P. e. canaster* by noting that iris color, instead of being red throughout the range of this subspecies, was variable — red, red-

dish or straw color. He also added notes on range to indicate that this form occupied most of Alabama, Georgia, northwestern Florida, and southern Mississippi and extended east to the coast of South Carolina. Koelz (1939: 122) suggested that the pale-eyed Florida and Georgia birds were sufficiently different from the dark-eyed birds of the north to be worthy of specific rank. By listing paratypes, from localities which he apparently felt were within the limits of geographic range, he outlined the extent of this population. Burleigh (1937: 459; 1944: 473–474) commented on the occurrence of the various races in the coastal areas of North Carolina and Mississippi. Worthington and Todd (1926: 219) contributed critical notes on the occurrence of intermediate specimens during the winter at Choctawhatchee Bay, Florida. Pearson, Brimley and Brimley (1942: 235) quoted pertinent correspondence from Alexander Wetmore concerning the distribution of *P. e. canaster, alleni* and *erythrophthalmus* in North Carolina. Ridgway (1901: 424) commented on east-west variation in *P. e. erythrophthalmus*. Oberholser (1938: 642–644) gave much information concerning the distribution of the Louisiana population for which he proposed the name *P. e. leptoleucus*. The range was indicated as including southeastern and central Louisiana. Birds from Baton Rouge and northward were referred to as *P. e. canaster*. Wetmore (1937a, b), Murphey (1937: 58), Howell (1928: 248–249), Allen (1871, 1872 and 1878), Ridgway (1901: 423–427) and Maynard (1881: 113) contributed much to the present knowledge of the species with comments on range, variation, measurements, migratory behavior, ecology, etc.

STATUS OF PROPOSED NAMES

Fringilla erythrophthalma Linnaeus

The status of this name after its proper placement in the genus *Pipilo* by Vieillot in 1819 is involved with that of *Pipilo erythrophthalmus canaster* Howell and is discussed under that heading.

Pipilo ater Vieillot

Vieillot proposed this name in 1819, to replace *Emberiza erythrophthalma* Latham. He also quotes Catesby and Wilson in his remarks. Since *Emberiza erythrophthalma* Latham is a synonym of *Fringilla erythrophthalma* Linn., *Pipilo ater* must also be a synonym of Linnaeus' name.

Pipilo alleni Coues vs. Pipilo leucopis Maynard

Despite the fact that Coues' action interfered with Maynard's intention of describing this form, *Pipilo alleni* Coues has priority over *Pipilo leucopis*. The original thought on the part of both Maynard and Coues as to the specific distinctness of this form has of course been shown in modern times to be fallacious, and its true status as a geographic race of *P. erythrophthalmus* is obvious.

Pipilo erythrophthalmus canaster Howell

Howell was certainly correct when he proposed that the Alabama birds were different from the form occurring in the northern part of the United States. It is unfortunate, however, that he did not investigate the status of the birds from the type locality of *P. e. erythrophthalmus*. Catesby (1731) may have had *P. e. canaster* at hand when he originally described the South Carolina form as *Passer niger, oculis rubris*. There are of course no Catesbian specimens available but the wording of the discussion of habits is such as to indicate that he was referring to the resident form occurring in South Carolina. Statements such as "a solitary bird," "one seldom sees them but in pairs," "they breed and abide all the year in Carolina in the shadiest woods," would indicate that he was aware of the summer conditions in this area. It is known that he made a trip up the Savannah River as far as Richmond County, Georgia. The greater portion of the geographic area of South Carolina has *canaster* as its breeding race today, and there is no indication that this condition has come about since the time of Catesby. Additionally, the included map in Catesby (1731) indicates that "Carolina" was taken to include a considerable area outside the present political boundaries of South Carolina. Despite this evidence I do not feel that it is worthwhile to re-arrange the names in this species at this time for the following reasons:

(1) Howell, the first reviser, chose to restrict Linnaeus' name to the northern population.

(2) The resultant confusion in the old literature coming about as the result of the change would outweigh the advantage of precise accuracy from a historical standpoint. Therefore I feel that it is preferable to retain the current usage of these names.

Pipilo erythrophthalmus leptoleucus Oberholser

This name, proposed by Oberholser for the towhees of New Orleans and vicinity, must be placed in synonomy with *P. e. canaster* Howell.

Fifteen topotypical males from Orleans Parish were available and they provide the following mean measurements with their standard errors: wing, 87.57 ± .81; tail, 93.29 ± .72; tail spot, 30.79 ± 1.19; culmen, 15.39 ± .09; width of lower mandible, 8.88 ± .06; tarsus, 27.67 ± .27; middle toe, 20.23 ± .21 mm. These means are not significantly different[1] from those found for *P. e. canaster*, and each of the specimens conforms in all measurements to the limits of variation of the latter. A single female was available and it is typical of *canaster*. Specimens examined in this connection are listed with those appearing under *P. e. canaster*, from Orleans Parish. Two of these, USNM 341594 and 363222, were apparently among those examined by Oberholser. Two others, USNM 340500 and LSU 1626 from St. Bernard and Assumption Parishes, respectively, are also mentioned by Oberholser as being referable to this race. I find that they are typical of *P. e. canaster*.

Pipilo alleni rileyi Koelz

In his original description Koelz stated that the red-eyed and pale-eyed forms were specifically distinct. He felt that this name should be applied to a population which was not a part of the red-eyed species occurring to the northward but rather a portion of the peninsular Florida form. His position in this may be well taken if means are discovered to allow a nomenclatorial differentiation of re-united populations as opposed to populations which are in the process of becoming distinct. It is certainly possible that the pale-eyed stock was at one time isolated from the continental population, although this situation no longer exists. There is no question that intergradation occurs between all adjacent forms. The characters involved in this situation, iris color, wing length, tail spot, etc., all show blending. At present there does not appear to be evidence to allow specific recognition of the pale-eyed forms, *alleni* and *rileyi*. Miller (1949: 338) discusses the problem of distinguishing between hybridization and intergradation. He concludes that hybridization implies lack of blended inheritance and that intergradation should be taken to indicate a blending of characters. Present day knowledge of genetic principles does not lend support to this suggestion.

Koelz was correct in his estimate of the validity of differences between the peninsular Florida population and the pale-eyed form occurring along the coast of North and South Carolina and in southeast Georgia. This form should be designated as *Pipilo erythrophthalmus rileyi* Koelz.

[1] These means fall within one standard error of the means of *P. e. canaster* except tarsus which falls within two standard errors.

THE SUBSPECIES OF PIPILO ERYTHROPHTHALMUS

Criteria Utilized

Much debate has gone on in regard to the proper rules and regulations which should be adopted by taxonomists in their recognition of subspecies. Most workers seem to agree that the subspecies level is certainly a subjective one, and yet much effort has been expended in an effort to reduce this problem to terms of objective criteria.

The advent of statistical study has of course been of much assistance in allowing the taxonomist to better estimate what might well be called the population phenotype from a relatively small sample of a population. It has also made it possible to better visualize the differences that exist between two or more populations. It seems that in addition to these benefits, however, statistical analysis leads the taxonomist into the feeling that the final equations will furnish an exact and clear answer to his problems. Indeed, on some occasions the statistics become the "end" rather than the "means." The fallacy is obvious — the units that are being dealt with are not numbers but rather simply measures of various expressions of certain genotypes and environments. The specimens concerned must be viewed as live animals, and the whole problem must remain in reality a biological one.

In ornithological studies in large part the taxonomist is dealing with continuous variates and with variation that appears graphically as a cline. Under such circumstances lines of demarcation between variant populations of necessity must be vague. There most certainly will be large portions of the populations that are not clearly identifiable.

Rand and Traylor (1950: 174) in their review of this problem conclude that five principal criteria of separability are in common use today:

1. The average of one subspecies separable from the average of the other subspecies.
2. 75 per cent of one separable from all of the other.
3. 50 per cent of one separable from all of the other.
4. 75 per cent of one separable from 75 per cent of the other.
5. The means of the two forms separable by the sum of their standard deviations (= 84 per cent from 84 per cent).

Amadon (1949), in summation of his discussion of this problem, adds to these "97 per cent from 97 per cent," which he recommends for adoption.

Rand and Traylor seem to lack the courage of their convictions (or the convictions themselves). They make a rather vague suggestion as to the degree of separability which should be demanded, *i.e.* about

80 to 90 per cent of one race separable from about 80 to 90 per cent of the other. They further fail to indicate whether this criterion of separation should be applied to statistical estimates of variability of the races or to particular samples at hand. From the examples given, unfortunately, it appears that the latter is the method used. In many cases this method may give a faulty impression of the limits of variability.

The problems that immediately arise in either case are manifold. Does the sample really represent the population? How large a geographic area may be visualized as the range of the races as opposed to the area of intergradation between the two? How large is the sample at hand? Is any subjective or mechanical bias present? Will naming the populations serve any useful purpose?

These problems are subjective ones and certainly no mathematical formulae will solve them. Under the circumstances it does not seem practical to try to establish any set degree of separability as the criterion for nomenclatorial recognition. In some cases if other factors, such as geographic area, are included, 50 per cent from 50 per cent separation might serve and in others 100 per cent from 100 per cent might not. Races must be visualized as transitory phenomena in the evolutionary development of the organism. The status of the populations as they are examined on the basis of contemporary specimens cannot be looked upon as a static situation. Existing environmental conditions may change, attended by morphological changes in the organism.

Another factor which must be considered, but which for the most part has been omitted from consideration, is the individual taxonomist's desire to name something. There seems to be little reason for doubting that this factor on many occasions has entered the picture, and there is reason to assume that the taxonomist is on some occasions biased in his conclusions by this factor.

It appears that in proposing criteria to be used in designation of subspecies the following should be paramount. Does naming the population serve any useful purpose? For example, is it possible in the case of migratory species to identify the breeding area of a winter-taken specimen? Is it possible to identify correctly a major portion of the population, not only in terms of "per cent from per cent," but in terms of area inhabited by identifiable populations versus area of intergradation? Is a clearer picture of relationships presented by furnishing the populations with names? In that these are subjective decisions it does not seem practical to follow Amadon in proposing an iron-clad degree of separability as the criterion. Some leeway must be observed in this respect, otherwise the whole structure of taxonomy

will suffer. Rand and Traylor's suggestion of about 80 to 90 per cent separability, if modified to about 80 per cent, may well be the most practical minimum — if the other subjective criteria mentioned are included.

In arriving at the conclusions presented here, following statistical analyses of variability, 75 per cent from 75 per cent has been the criterion of separability utilized. Other considerations, however, have been included. This is evidenced by my declining to name the eastern and western segments of the population designated as *P. e. erythrophthalmus,* despite the fact that in males, 74.5 per cent separation is obtained on the basis of tail and length of wing.[1] In this case the fact that a major portion of the range of the form here designated as *erythrophthalmus* would be inhabited by intermediate, unidentifiable birds seems to overrule the desirability of such action (Map 1). In the four subspecies recognized a minimum of 75 per cent separability obtains, and in addition the areas of intergradation are small (Map 2). There is also correlation of morphological variation with environmental and physiographic differences, and a reasonable phylogenetic picture may be visualized.

Keys to Subspecies

In the keys which follow, the index characters are listed in the order of diminishing degree of separation. In all cases the first character mentioned in each couplet furnishes at least 75 per cent separation.

Iris color of birds in first winter plumage presents certain difficulty in the use of these keys, since the iris may not yet have taken on the adult appearance. As mentioned in another connection in this report, *alleni* and *rileyi* both have grayish irides at this time, whereas *erythrophthalmus* and *canaster* have brownish irides.

Adult Males

1. Wing usually less than 83.0 mm., tail spot usually less than 23.0 mm., tarsus usually less than 27.5 mm., middle toe usually less than 19.5 mm., iris straw colored . . . . . *alleni*

1a. Wing usually 83.0 mm. or more, tail spot usually 23.0 mm. or more, tarsus usually 27.5 mm. or more, middle toe usually 19.5 mm. or more, iris variable in color 2

2. Iris usually straw, buff or yellow (sometimes orange), tail spot usually less than 28.2 mm. (usually more than 23.0 mm.) . . . . . *rileyi*

[1] This degree of separability is inversely related to geographic area — the larger the area, the less separability. It reaches its maximum when samples from widely separated localities are compared. For example, 84 per cent of North Dakota, Iowa, Minnesota and Wisconsin were separable from a series taken on Long Island, New York.

2a. Iris variable but usually red, tail spot usually 28.2 mm. or more.....3
3. Culmen usually less than 15.0 mm., tail spot/tail ratio usually 36.0 per cent or more, iris red.....*erythrophthalmus*
3a. Culmen usually 15.0 mm. or more, tail spot/tail ratio usually less than 36.0 per cent, iris usually red but sometimes orange, buff or yellow.....*canaster*

Adult Females

1. Tail spot usually less than 19.5 mm., wing usually less than 78.0 mm., iris straw.....*alleni*
1a. Tail spot usually 19.5 mm. or more, wing usually 78.0 mm. or more, iris variable.....2
2. Iris usually straw, buff or yellow (sometimes orange), wing usually 82.1 mm. or less (more than 78.0 mm.), tail spot usually less than 24.6 mm.....*rileyi*
2a. Iris usually red (sometimes orange, buff or yellow), wing usually 82.2 mm. or more, tail spot usually 24.6 mm. or more.....3
3. Tail spot/tail ratio usually 30.3 per cent or more, tail spot usually 28.7 mm. or more, culmen usually 14.8 mm. or less, tarsus 27.2 mm. or more, iris red.....*erythrophthalmus*
3a. Tail spot/tail ratio usually less than 30.3 per cent, tail spot usually less than 28.7 mm., culmen usually more than 14.8 mm., tarsus usually less than 27.2 mm., iris usually red but sometimes orange, buff or yellow.....*canaster*

Pipilo erythrophthalmus erythrophthalmus Linnaeus

Fringilla erythrophthalmus Linnaeus (1758: 180), description based on Catesby (Vol. 1: 34, pl. 34). Type locality: South Carolina.
Pipilo ater Vieillot (1819: 292).
Pipillo erythrophthalmus, Vieillot (1824: 109, pl. 80).
Pipilo erythrophthalmus var. *erythrophthalmus*, Baird, Brewer, and Ridgway (1874: 108).

Description

Diagnosis. A large, small-billed, vividly colored, red-eyed form, showing a large amount of white on the rectrices.

Average dimensions of males. Wing, 87.57 ± .15 (σ, 2.77); tail, 92.91 ± .20 (σ, 3.82); culmen, 14.49 ± .03 (σ, 0.58); width of lower mandible, 8.68 ± .02 (σ, 0.29); tarsus, 27.37 ± .05 (σ, 0.90); middle toe without claw, 19.64 ± .04 (σ, 0.71); length of white on inner web of outermost rectrix, 36.70 ± .24 (σ, 4.47); tail spot/tail ratio, 39.36 ± .27 (σ, 4.96). (See Table 1.)

Average dimensions of females. Wing, 83.38 ± .28 (σ, 2.68); tail, 88.22 ± .41 (σ, 3.80); culmen, 14.47 ± .62 (σ, 0.07); width of lower mandible, 8.60 ± .04 (σ, 0.33); tarsus, 26.60 ± .10 (σ, 0.96); middle toe without claw, 19.06 ± .07 (σ, 0.71); length of white on inner web of outermost rectrix, 33.18 ± .46 (σ, 4.29); tail spot/tail ratio, 37.47 ±.51 (σ, 4.67). (See Table 2.)

Table 1
P. e. erythrophthalmus
Males

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	359	87.57	.15	2.77	84.81–90.34	80.0– 96.0
Tail	351	92.91	.20	3.82	89.09–96.73	82.0–104.0
Tail Spot	345	36.70	.24	4.47	32.23–41.17	23.6– 55.0
Culmen	350	14.49	.03	.58	13.92–15.07	13.1– 16.0
Mandible Width	346	8.68	.02	.29	8.39– 8.97	7.5– 9.5
Tarsus	355	27.37	.05	.90	26.48–28.27	24.8– 29.5
Middle Toe	351	19.64	.04	.71	18.93–20.35	17.4– 22.4
Tail Spot/Tail	340	39.36	.27	4.96	34.40–44.32	26.0– 61.0

Table 2
P. e. erythrophthalmus
Females

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	95	83.38	.28	2.68	80.70–86.06	77.0–89.5
Tail	90	88.22	.41	3.80	84.42–92.03	78.0–96.5
Tail Spot	90	33.18	.46	4.29	28.90–37.47	24.6–45.3
Culmen	91	14.47	.07	.62	13.85–15.09	13.0–15.4
Mandible Width	90	8.60	.04	.33	8.27– 8.94	7.8– 9.4
Tarsus	90	26.60	.10	.96	25.64–27.57	24.0–29.0
Middle Toe	92	19.06	.07	.71	18.36–19.77	17.0–20.4
Tail Spot/Tail	85	37.47	.51	4.67	32.81–42.14	28.0–55.0

Average color of males.[1] Back, Sooty Black; flanks, 5-D-12; breast, Sooty Black; top of head, Sooty Black.

Average color of females. Back, 15-J-8; flanks, 13-H-12; breast, 14-K-9; top of head, 8-L-12.

Iris Color. Red.

Breeding range. Transition and Upper Austral zones east of the Great Plains from southern Saskatchewan, southern Manitoba, southern Ontario and southern Maine, south through middle North Dakota, Iowa, Kansas and northern Arkansas, east through middle Tennessee and northern Georgia and western South Carolina to the Atlantic coast in southern Virginia (Princess Anne County). Casual in New Brunswick. (See Map 2.)

Winter range. From southeast Texas, Louisiana, Mississippi, Tennessee and North Carolina south to the Gulf Coast and mid-peninsular Florida. Occasionally as far north as southeastern Nebraska, Iowa, Wisconsin, Illinois, southern Michigan, Ohio, Pennsylvania, southern New York and Massachusetts. (See Map 3.)

Comments. During the winter months this towhee moves south into the ranges of the other three races, extending well down into peninsular Florida in the east and into east Texas in the west. During this season it is prone to congregate in flocks of 10–15 individuals and is often seen in company with the resident form of the locality in which it is spending the winter. When in Florida *P. e. erythrophthalmus* prefers much heavier cover than does *P. e. alleni* and it is most regularly seen along the edges of fairly dense hardwood hammocks. It does not appear to be unusual for some individuals to remain in the breeding area during the winter. Numerous published records attest to this, and in the material examined by me seven individuals were taken in the north during the winter months.

Specimens Examined

Atypical specimens are indicated as follows:
**erythrophthalmus* > *canaster*
***erythrophthalmus* > *rileyi*

Breeding Males.[2] ARKANSAS: Washington Co., 4 (AMNH). CONNECTICUT: Fairfield Co., 3 (AMNH); New Haven Co., 2 (AMNH). GEORGIA: Fannin Co., 1 (MMP), 2 (USNM); Habersham Co., 1 (USNM); Rabun Co., 4 (USNM), 1 (LSU); Townes Co.,

[1] For explanation of color nomenclature see discussion on p. 329.

[2] Breeding material includes all those individuals utilized in arriving at the estimates of the characters of the population. For this reason some atypical specimens are included under this heading.

1*(USNM); Union Co., 1*(MMP), 2 (USNM); White Co., 1 (USNM). ILLINOIS: Cook Co., 4 (CNHM); Fulton Co., 1 (CNHM); Lake Co., 1 (AMNH); Marshall Co., 1 (CNHM); Pulaski Co., 4 (CNHM); Will Co., 7 (CNHM). INDIANA: Knox Co., 1 (AMNH); Lake Co., 1 (CNHM); Marion Co., 1 (UMMZ); Wells Co., 2 (CNHM). IOWA: Linn Co., 1 (CNHM); Marion Co., 1 (AMNH). KENTUCKY: Madison Co., 1 (USNM); Union Co., 1 (USNM); Harlan Co., 1 (USNM). MARYLAND: Montgomery Co., 1 (CM); Prince George Co., 1 (AMNH). MASSACHUSETTS: Barnstable Co., 1 (AMNH); Hampshire Co., 1 (AMNH); Middlesex Co., 4 (AMNH); Norfolk Co., 1 (AMNH), 1 (USNM). MICHIGAN: Berrien Co., 1 (UMMZ); Calhoun Co., 1 (UMMZ); Charlevoix Co., 3 (UMMZ); Cheboygan Co., 1 (MMP); Chippewa Co., 1 (UMMZ); Huron Co., 1 (UMMZ); Ionia Co., 1 (AMNH); Kalamazoo Co., 2 (UMMZ); Livingston Co., 3 (UMMZ); Menominee Co., 1 (UMMZ); Oscoda Co., 1 (UMMZ); Washtenaw Co., 4 (MMP), 3 (GMS), 3 (UMMZ); Wexford Co., 1 (AMNH). MINNESOTA: Hennepin Co., 1 (AMNH); Olmstead Co., 2 (AMNH). MISSOURI: Wayne Co., 1 (USNM). NEW HAMPSHIRE: Hillsboro Co., 1 (AMNH). NEW JERSEY: Bergen Co., 4 (AMNH); Essex Co., 4 (AMNH); Mercer Co., 1 (AMNH); Middlesex Co., 1 (AMNH); Morris Co., 2 (AMNH); County Unknown, 2 (AMNH). NEW YORK: Erie Co., 1 (AMNH); Jefferson Co., 1 (AMNH); Kings Co., 3 (AMNH); Nassau Co., 1 (MMP), 7 (AMNH); New York Co., 3 (AMNH); Orange Co., 1 (AMNH), 4 (USNM); Putnam Co., 1 (AMNH); Queens Co., 15 (AMNH); Rensselaer Co., 1 (AMNH); Richmond Co., 1 (AMNH); Rockland Co., 3 (AMNH); Suffolk Co., 1 (CM), 1 (UMMZ), 52 (AMNH); Westchester Co., 6 (AMNH). NORTH CAROLINA: Buncombe Co., 5 (USNM); Burke Co., 1 (USNM); Cherokee Co., 1* (USNM); Greenville Co., 1 (USNM); Jackson Co., 1 (MCZ); Macon Co., 1* (USNM), 2 (USNM), 1* (DZUG), 6 (DZUG); Sampson Co., 1 (USNM); Transylvania Co., 2 (USNM); Watauga Co., 2 (USNM); Yancey Co., 1* (USNM), 2 (USNM). NORTH DAKOTA: Towner Co., 1 (CNHM), 6 (UMMZ). OHIO: Portage Co., 1 (AMNH). PENNSYLVANIA: Beaver Co., 7 (CM); Bedford Co., 1 (CM); Blair Co., 1 (AMNH); Butler Co., 1 (CM); Cambria Co., 1 (AMNH), 2 (CM); Columbia Co., 1 (CM); Crawford Co., 3 (CM); Erie Co., 2 (AMNH); Fayette Co., 1 (LSU); Pike Co., 1 (AMNH); Washington Co., 1 (CM). RHODE ISLAND: Providence Co., 4 (AMNH). SOUTH CAROLINA: Anderson Co., 1 (USNM); Cherokee Co., 1 (USNM); Greenville Co., 2 (CHAM), 1* (USNM), 1 (USNM), 1* (AMNH), 2 (AMNH); Pickens Co., 2* (USNM). TENNESSEE: Anderson Co., 1 (USNM); Campbell Co., 2 (UMMZ); Cocke Co., 1 (USNM); Cum-

berland Co., 1 (USNM); Johnson Co., 5 (USNM); Munroe Co., 1 (UMMZ); Sullivan Co., 1 (USNM); Van Buren Co., 1 (USNM). VIRGINIA: Accomac Co., 4* (USNM), 1 (USNM); Arlington Co., 1 (AMNH); Augusta Co., 3 (USNM); Fairfax Co., 1* (AMNH), 1 (AMNH); Highlands Co., 2 (USNM); Norfolk Co., 1 (LSU), 1* (USNM); Northampton Co., 2 (USNM); Princess Anne Co., 1* (UMMZ); Rockbridge Co., 5 (USNM); Smythe Co., 1 (USNM); Spotsylvania Co., 1 (USNM); Wythe Co., 4 (MCZ). VERMONT: Wyndham Co., 1 (AMNH). WASHINGTON, D. C.: 2 (CM). WEST VIRGINIA: Calhoun Co., 1 (USNM); Barbour Co., 1 (USNM); Brooke Co., 1 (MMP); Nicholas Co., 1 (USNM); Pendleton Co., 1 (MMP); Pocohontas Co., 2 (USNM); Randolph Co., 1 (USNM); Tucker Co., 1 (UMMZ), 1 (USNM). WISCONSIN: Burnett Co., 1 (USNM); Dodge Co., 7 (CNHM); Juneau Co., 2 (AMNH); Rock Co., 1 (FSM); Walworth Co., 3 (AMNH); ?Selinctous? 1 (CM).

Breeding females. CONNECTICUT: New Haven Co., 2 (AMNH). GEORGIA: Habersham Co., 1 (USNM); Rabun Co., 1 (USNM); Townes Co., 2 (USNM); White Co., 1* (USNM). KENTUCKY: Harlan Co., 1 (USNM); Union Co., 1 (USNM). MARYLAND: Montgomery Co., 5 (USNM); Prince George Co., 1 (AMNH). MASSACHUSETTS: Barnstable Co., 1 (AMNH); Middlesex Co., 1 (AMNH). MICHIGAN: Berrien Co., 1 (UMMZ); Charlevoix Co., 2 (UMMZ); Chippewa Co., 1 (UMMZ); Huron Co., 1 (UMMZ); Jackson Co., 2 (UMMZ); Kalamazoo Co., 1 (UMMZ); Lapeer Co., 1 (UMMZ); Leelanau Co., 1 (UMMZ); Washtenaw Co., 4 (MMP), 1 (GMS). NEW YORK: Kings Co., 1 (AMNH); Nassau Co., 2 (AMNH), 1 (USNM); Orange Co., 2 (AMNH); Queens Co., 2 (AMNH); Suffolk Co., 7 (AMNH), 1 (UMMZ). NORTH CAROLINA: Buncombe Co., 1 (LSU), 1 (USNM); Macon Co., 1 (MCZ); Sampson Co., 1 (USNM); Wake Co., 1 (NCS); Watauga Co., 1 (USNM). NORTH DAKOTA: Towner Co., 3 (UMMZ). PENNSYLVANIA: Beaver Co., 1 (CM); Cambria Co., 1 (CM); Crawford Co., 1 (CM); Westmorland Co., 2 (CM). SOUTH CAROLINA: Greenville Co., 2 (AMNH), 1 (CHAM), 1 (USNM). TENNESSEE: Cocke Co., 1 (USNM); Cumberland Co., 1* (USNM), 1 (USNM); Johnson Co., 1 (USNM). VIRGINIA: Accomac Co., 1 (USNM); Arlington Co., 1 (AMNH); Giles Co., 1 (AMNH), 2 (MCZ); Highlands Co., 2 (USNM); North Hampton Co., 1 (CM); Elliot Knob, 1 (USNM). WASHINGTON, D. C.: 1 (AMNH), 2 (CM), 1 (USNM). WEST VIRGINIA: Barbour Co., 1 (USNM); Ohio Co., 1 (MMP); Randolph Co., 1 (USNM); Tucker Co., 1 (AMNH), 1 (GMS); Zeld, 1 (USNM). WISCONSIN: Vilas Co., 1 (USNM); Walworth Co., 2 (AMNH).

Wintering Males.[1] ALABAMA: Autauga Co., 1 (USNM); Houston Co., 1* (USNM); Montgomery Co., 2 (USNM). ARKANSAS: Crawford Co., 1 (USNM). FLORIDA: Alachua Co., 1 (AMNH), 4 (FSM), 1 (JCD); Citrus Co., 1 (FSM); Duval Co., 2 (MCZ), 4 (USNM); Escambia Co., 2 (USNM); Leon Co., 1* (CNHM), 1 (CNHM); Levy Co., 1 (AMNH), 1 (MCZ), 1 (JCD); Nassau Co., 3 (AMNH); Okaloosa Co., 7 (CM); Okeechobee Co., 1 (USNM); Pinellas Co., 1 (MCZ); Polk Co., 1 (USNM); Putnam Co., 2 (USNM); 2 (CNHM); St. Johns Co., 2 (AMNH); Santa Rosa Co., 8 (CM); Wakulla Co., 2 (USNM), 1* (USNM), 2 (FSM), 1 (JCD). GEORGIA: Barrow Co., 1 (USNM); Bibb Co., 1 (USNM); Camden Co., 1 (MCZ); Catoosa Co., 1 (USNM); Charlton Co., 3 (USNM); Chatham Co., 2 (MCZ); 1 (USNM); Cherokee Co., 1 (USNM); Clarke Co., 8 (USNM), 1* (USNM); Cobb Co., 1 (CNHM); De Kalb Co., 5 (USNM), 2* (USNM); Early Co., 1 (USNM); Fulton Co., 6 (USNM); Glynn Co., 1(MCZ); Hall Co., 1 (USNM); Heard Co., 1 (USNM); McIntosh Co., 1 (AMNH); Thomas Co., 1 (AMNH), 1 (USNM). KENTUCKY: Butler Co., 1 (USNM). LOUISIANA: Cameron Parish, 1 (LSU); East Baton Rouge Parish, 2 (CNHM), 4 (LSU), 1* (LSU), 1 (USNM); Ouachita Parish, 1 (LSU); Orleans Parish, 1* (LSU), 2 (USNM); West Feliciana Parish, 2 (LSU). MARYLAND: Worcester Co., 1 (USNM). MISSISSIPPI: Bolivar Co., 1 (CNHM); Harrison Co., 6 (USNM), 4 (LSU); Warren Co., 2 (LSU). NEW JERSEY: Morris Co., 1 (AMNH). NORTH CAROLINA: Brunswick Co., 1 (NCS); Buncombe Co., 3 (USNM), 1 (MCZ); Carteret Co., 1 (USNM); Robeson Co., 1 (CNHM); Transylvania Co., 2 (USNM); Yancey Co., 1 (USNM). OHIO: Pickaway Co., 1 (AMNH). SOUTH CAROLINA: Beaufort Co., 2 (MCZ); Berkeley Co., 1 (CHAM); Charleston Co., 5 (CHAM), 1 (LSU), 1 (USNM); Horry Co., 1 (CHAM); Kershaw Co., 5 (USNM); Pickens Co., 1 (CHAM). TENNESSEE: Giles Co., 2 (USNM); Hamilton Co., 1 (USNM); Shelby Co., 3 (LSU). TEXAS: Lee Co., 1 (AMNH); Nueces Co., 1 (AMNH). WEST VIRGINIA: Brooke Co., 1 (GMS); Cabell Co., 1 (USNM).

Wintering females. ALABAMA: Autauga Co., 1 (USNM); Jackson Co., 1* (USNM); Ardell, 2 (USNM); Orange Beach, 1 (USNM). FLORIDA: Alachua Co., 2 (FSM), 1 (JCD); Duval Co., 1 (MCZ); Levy Co., 1* (MCZ); Okaloosa Co., 5 (CM); Okechobee Co., 1 (USNM); Santa Rosa Co., 2 (CNHM), 1* (CNHM); Volusia Co., 1 (MCZ); Wakulla Co., 5 (USNM), 3 (FSM); Cow Creek, 1* (CNHM). GEORGIA: Clarke Co., 2 (MMP), 1 (USNM); Charlton Co., 1

[1] Wintering and migrant specimens were identified as individuals on the basis of physical characteristics.

(USNM); Echols Co., 1 (USNM); Richmond Co., 1 (USNM); Blackbeard Island, 1 (USNM). KENTUCKY: Hopkins Co., 1 (USNM). LOUISIANA: Baton Rouge Parish, 1 (CNHM), 2 (LSU); Orleans Parish, 1 (LSU), 1 (USNM); Ouachita Parish, 1 (LSU); St. John the Baptist Parish, 1 (LSU); Washington Parish, 1 (LSU); Chef Menteur, 1 (CNHM). MISSISSIPPI: Harrison Co., 4 (USNM), 1 (LSU); Jackson Co., 1 (CNHM); Warren Co., 1 (LSU); Lobdell, 1 (LSU). NORTH CAROLINA: Buncombe Co., 1 (USNM); Pasquotank Co., 1 (USNM); Rockingham Co., 1* (USNM); Wayne Co., 1 (USNM). SOUTH CAROLINA: Charleston Co., 1 (CHAM); Georgetown Co., 1 (USNM); Kershaw Co., 1 (USNM), 1* (USNM). TENNESSEE: Giles Co., 1 (USNM); Roane Co., 1 (USNM). TEXAS: Bee Co., 1 (AMNH); Cook Co., 1 (USNM); Galveston Co., 1 (AMNH). Hardin Co., 1 (AMNH). WEST VIRGINIA: Brooke Co., 1 (GMS).

Migrant Males. ALABAMA: Jackson Co., 1 (USNM); Tuscaloosa Co., 1 (USNM). CONNECTICUT: Windham Co., 2 (AMNH). FLORIDA: Alachua Co., 1 (DBUF); Dixie Co., 1 (FSM); Escambia Co., 1* (LSU); Nassau Co., 1 (AMNH); Wakulla Co., 1 (FSM). GEORGIA: Bullock Co., 1 (DZUG); Camden Co., 3 (MCZ); Chatham Co., 1* (USNM), 1 (USNM); Clarke Co., 7 (USNM); Cobb Co., 5 (CNHM), 1 (MMP); De Kalb Co., 1 (USNM); Fannin Co., 1 (USNM); Hall Co., 1 (USNM); Liberty Co., 1 (USNM); Thomas Co., 1 (AMNH); Union Co., 1 (USNM). ILLINOIS: Wabash Co., 1 (AMNH). KENTUCKY: Bell Co., 3 (USNM); Carroll Co., 1 (USNM); Hopkins Co., 1 (USNM); Rockcastle Co., 1 (USNM); Rowan Co., 1 (USNM); Trigg Co., 1 (USNM). LOUISIANA: East Baton Rouge Parish, 2 (LSU), 1* (LSU). MARYLAND: Cecil Co., 1 (AMNH); Montgomery Co., 2 (AMNH), 2 (CM); Prince George Co., 1 (AMNH). NEBRASKA: Lancaster Co., 1 (AMNH); Bald Island, 1 (USNM). NEW YORK: New York Co., 1 (AMNH); Queens Co., 1 (GMS); Suffolk Co., 2 (AMNH). NORTH CAROLINA: Buncombe Co., 1 (AMNH); Dare Co., 1 (USNM); Iredell Co., 1 (USNM); Pasquotank Co., 1 (USNM); Wake Co., 3 (NCS). PENNSYLVANIA: Erie Co., 1 (CM). SOUTH CAROLINA: Charleston Co., 4 (MCZ), 1 (CNHM); Cherokee Co., 1* (USNM); Georgetown Co., 1 (USNM); Richland Co., 1 (CNHM). TENNESSEE: Fayette Co., 2 (USNM); Lake Co., 1 (USNM); Lincoln Co., 1 (USNM); Obion Co., 1 (USNM); Roane Co., 2 (USNM); Stewart Co., 1 (USNM). VIRGINIA: Alexandria Co., 3 (USNM); Arlington Co., 1 (USNM); Essex Co., 1 (USNM); Fairfax Co., 2* (MCZ), 5 (USNM); Orange Co., 1 (USNM). WEST VIRGINIA: Cabell Co., 1 (USNM); Greenbriar Co., 1 (AMNH); Logan Co., 1 (USNM).

Migrant Females. ALABAMA: Colbert Co., 2 (USNM); Walker Co., 1 (USNM); Sand Mt. 1 (USNM). FLORIDA: Alachua Co., 2 (FSM), 1 (JCD); Wakulla Co., 1 (FSM). GEORGIA: Chatham Co., 1 (MCZ); Clarke Co., 1 (USNM); Cobb Co., 1 (CNHM). ILLINOIS: Wabash Co., 1 (USNM). KENTUCKY: Carroll Co., 1 (USNM); Mead Co., 1 (USNM); Trigg Co., 1 (USNM). LOUISIANA: Orleans Parish, 1 (LSU). MICHIGAN: Jackson Co., 1 (GMS). MISSISSIPPI: Bolivar Co., 1 (USNM), 1* (USNM); Harrison Co., 2 (LSU), 4 (USNM). NEW JERSEY: Morris Co., 1 (AMNH). NEW YORK: Orange Co., 1 (USNM); Queens Co., 1 (AMNH); Dunwoodie, 1 (AMNH). NORTH CAROLINA: Charleston Co., 2 (USNM). TENNESSEE: Carter Co., 1* (USNM); Roane Co., 1 (USNM); Shelby Co., 1 (USNM); Union Co., 1 (UMMZ). TEXAS: Chambers Co., 1 (AMNH). VIRGINIA: Fairfax Co., 2 (USNM); Surrey Co., 1 (USNM). WASHINGTON, D. C.: 1 (USNM). WEST VIRGINIA: Cabell Co., 1 (USNM); Logan Co., 1 (USNM); Pendleton Co., 1 (USNM); Rorer, 1 (CM); Fourleen, 1 (USNM).

Pipilo erythrophthalmus alleni Coues

Pipilo alleni Coues (1871: 366, footnote), original description. Type locality: Dummitt's Grove, Indian River, Florida.

Pipilo erythrophthalmus var. *alleni*, Baird, Brewer, and Ridgway (1874: 112).

Pipilo leucopis Maynard (1878: 113, pl. IV), original description. Type locality: Dummitt's Grove, Florida.

Pipilo erythrophthalmus subsp. *Pipilo alleni*, Sharpe (1888: 746).

Description

Diagnosis. A small, medium-billed, pale-eyed race, showing very little white on the rectrices.

Average dimensions of males. Wing, 80.47 ± .29 (σ, 2.62); tail, 91.43 ± .42 (σ, 3.74); exposed culmen, 15.05 ± .07 (σ, 0.61); width of lower mandible, 8.48 ± .04 (σ, 0.33); tarsus, 26.78 ± .11 (σ, 0.95); middle toe without claw, 18.88 ± .09 (σ, 0.81); length of white on inner web of outermost rectrix, 19.71 ± .50 (σ, 4.44). (See Table 3).

Average dimensions of females. Wing, 76.50 ± .41 (σ, 2.08); tail, 85.42 ± .67 (σ, 3.40); exposed culmen, 14.71 ± .10 (σ, 0.48); width of lower mandible, 8.47 ± .06 (σ, 0.28); tarsus, 25.89 ± .17 (σ, 0.89); middle toe without claw, 18.57 ± .14 (σ, 0.71); length of white on inner web of outermost rectrix, 15.58 ± .69 (σ, 3.52). (See Table 4.)

Average color of males. Back, Iron Gray; flanks ,12-F-10; breast, Iron Gray; top of head, Iron Gray.

Average color of females. Back, 15-E-7; flanks, 13-D-11; breast, 14-J-9; top of head, 15-E-12.

Table 3
P. e. alleni
Males

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	82	80.47	.29	2.62	77.85–83.08	73.0– 89.0
Tail	81	91.43	.42	3.79	87.69–95.17	78.0–102.2
Tail Spot	78	19.71	.50	4.44	15.26–24.15	6.1– 27.5
Culmen	80	15.05	.07	.61	14.44–15.65	13.9– 16.1
Mandible Width	82	8.48	.04	.33	8.15– 8.81	7.6– 9.5
Tarsus	81	26.78	.11	.95	25.84–27.73	24.7– 29.1
Middle Toe	81	18.88	.10	.81	18.07–19.70	17.0– 21.0

Table 4
P. e. alleni
Females

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	26	76.50	.41	2.08	74.42–78.58	73.0–81.5
Tail	26	85.43	.67	3.40	82.03–88.82	79.3–92.1
Tail Spot	26	15.58	.69	3.52	12.06–19.09	6.0–20.2
Culmen	25	14.71	.10	.48	14.23–15.19	13.1–15.5
Mandible Width	22	8.47	.06	.28	8.19– 8.74	8.0– 9.0
Tarsus	26	25.89	.17	.89	25.00–26.77	24.2–28.0
Middle Toe	26	18.57	.14	.71	17.85–19.28	17.0–20.0

Iris color. Straw.

Breeding range. Florida (from Bay, Franklin, Levy, Alachua and Putnam Counties south through the peninsula); absent from the Florida Keys. (See Map 2.)

Winter range. In Florida (from Santa Rosa, Franklin, Leon, Columbia and Duval Counties south through the peninsula); absent from the Florida Keys. (See Map 3.)

Comments. *P. e. alleni* is the best defined of the four races of *P. erythrophthalmus*. The uniformity of iris color, small amount of white on the outermost rectrix and the short wing make this race easily recognized.

Its habitat preference during the breeding season varies with locality. Along the coast the towhee is the commonest bird of the dune association of *Quercus geminata, Q. myrtifolia, Pinus clausa, Serenoa repens* and *Ceratiola ericoides*. This same scrub habitat, inland, is also heavily populated with *P. e. alleni*. In areas where scrub does not occur the birds are found in second-growth associations which approximate the natural scrub habitat in physical aspect. Often large numbers are found in close proximity to cities and towns, where cultivation has created similar conditions.

During the winter *alleni* does not seem to be so specific in its habitat demands, and is found in a great variety of situations. Individuals have been taken in urban areas, pine flatwoods, mesophytic hammocks, tropical hammocks and mangrove bays. During this season flocks of fifteen or twenty birds are not uncommon and on some occasions these flocks may contain resident and migrant individuals.

Specimens Examined

Atypical specimens are indicated as follows:

**alleni > rileyi*

Breeding Males. FLORIDA: Alachua Co., 1 (AMNH), 1 (BDUF), 2 (PB), 2 (JCD); Bay Co., 1* (UMMZ); Brevard Co., 3 (AMNH), 3 (CNHM), 1* (CNHM), 1 (USNM), 2 (MCZ), 1 (PB), 1 (JCD); Broward Co., 2 (PB), 1 (JCD); Charlotte Co., 2 (CM); Collier Co., 1 (USNM); Dade Co., 1 (JCD), 1 (USNM), 1 (UMMZ); Franklin Co., 1 (LSU), 2 (JCD), 1* (JCD); Highlands Co., 1 (USNM); Hillsborough Co., 4 (JCD); Lee Co., 3 (JCD); Levy Co., 3 (JCD); Martin Co., 1 (JCD); Palm Beach Co., 1 (CM), 1 (USNM); Pasco Co., 2 (USNM); Pinellas Co., 4 (MCZ); 1 (UMMZ), 2 (AMNH), 4 (USNM); Polk Co., 5 (JCD); Putnam Co., 4 (GN), 1 (USNM), 1* (JCD); Saint Lucie Co., 1 (AMNH); Sarasota Co., 1 (AMNH); Volusia Co., 6 (AMNH).

Breeding Females. FLORIDA: Alachua Co., 1 (JCD); Benton, 1 (USNM); Brevard Co., 1 (AMNH); Broward Co., 4 (JCD); Charlotte Co., 1 (CM); 1 (JCD); Hillsborough Co., 2 (JCD); Highlands Co., 1 (LSU); Levy Co., 2 (JCD); Nassau Co., 1 (USNM); Orange Co., 1 (CM); Pinellas Co., 1 (AMNH), 1 (MCZ); 4 (USNM); Polk Co., 1 (JCD); Putnam Co., 1 (GN); Volusia Co., 1 (AMNH), 1 (MCZ).

Wintering Males. FLORIDA: Alachua Co., 3 (AMNH), 1* (AMNH), 4 (JCD), 1(PB); Brevard Co., 1 (MMP), 1 (MCZ), 3 (CNHM), 1* (CM), 2 (USNM), 18 (AMNH); Charlotte Co., 1 (UMMZ), 9 (MCZ); Collier Co., 1 (MMP), 4 (USNM); Columbia Co., 2 (LSU); Escambia Co., 1* (LSU); Franklin Co., 1 (LSU); Hernando Co., 1 (JCD), 1 (PB); Highlands Co., 6 (USNM); Hillsborough Co., 1 (CM); Indian River Co., 1 (LSU); Lake Co., 1 (JCD); Lee Co., 2 (AMNH), 4 (CNHM); Leon Co., 1 (USNM); Levy Co., 2 (MCZ), 1* (MCZ), 1 (PB), 2 (JCD), 6 (AMNH), 1* (AMNH); Nassau Co., 3 (CNHM), 1* (CNHM); Okaloosa Co., 1 (USNM); Okeechobee Co., 3 (USNM); Orange Co., 3 (GMS); Osceola Co., 3 (USNM), 1* (USNM); Palm Beach Co., 5 (CNHM); Pinellas Co., 4 (AMNH), 4 (MCZ), 1* (MCZ), 2 (CNHM), 1 (FSM), 7 (UMMZ); Polk Co., 1 (USNM), 2 (UMMZ); Putnam Co., 3 (CNHM), 1* (CNHM); Santa Rosa Co., 2 (CNHM), 2* (CNHM); St. Lucie Co., 1 (USNM); Volusia Co., 2 (AMNH), 1 (MCZ). GEORGIA: Camden Co., 1* (AMNH), 1* (MCZ), 1 (USNM); Chatham Co., 1* (LSU); Liberty Co., 1* (DZUG), 1* (USNM).

Wintering Females. FLORIDA: Brevard Co., 1 (AMNH), 3 (CNHM), 1* (CNHM); Collier Co., 2 (USNM); Dade Co., 1 (UMMZ); Desoto Co., 2 (USNM); Duval Co., 1* (MCZ); Franklin Co., 1 (MMP), 1 (LSU); Highlands Co., 1 (USNM); Indian River Co., 3 (MCZ); Lee Co., 1 (CNHM), 6 (MCZ); Nassau Co., 1 (CNHM); Orange Co., 1 (GMS); Osceola Co., 1 (USNM); Okaloosa Co., 1 (USNM); Palm Beach Co., 1 (USNM), 2 (CNHM); Pinellas Co., 1 (AMNH), 1 (CNHM), 4 (UMMZ), 1* (UMMZ), 3 (MCZ); Putnam Co., 3 (CNHM); Santa Rosa Co., 2 (CNHM), 4* (CNHM); Volusia Co., 2 (MCZ), 1 (AMNH); Kissimmee Prairie, 1 (USNM), 1 (MCZ). GEORGIA: Camden Co., 1* (MCZ); Chatham Co., 1* (CHAM); Levy Co., 1* (MCZ).

Migrant Females. FLORIDA: Brevard Co., 1 (CNHM); Lee Co., 1 (MCZ); Orange Co., 1 (MMP); Palm Beach Co., 2 (CNHM); Pinellas Co., 1 (MCZ), 1 (UMMZ).

Pipilo erythrophthalmus canaster Howell

Pipilo erythrophthalmus var. *erythrophthalmus*, Baird, Brewer, and Ridgway (1874: 108), part.

Pipilo erythrophthalmus canaster Howell (1913: 202), original description. Type locality: Spring Hill, Alabama.

Pipilo erythrophthalmus leptoleucus Oberholser (1938: 641), original description. Type locality: New Orleans, Louisiana.

Description

Diagnosis. A large, large-billed, pale race, with variable eye color, showing a medium amount of white on the rectrices.

Average dimensions of males. Wing, 87.30 ± .21 (σ, 2.50); tail, 94.95 ± .30 (σ, 3.53); culmen, 15.44 ± .05 (σ, 0.60); width of lower mandible, 8.94 ± .03 (σ, 0.37); tarsus, 20.19 ± .08 (σ, 1.00); middle toe without claw, 20.19 ± .07 (σ, 0.88); length of white on inner web of outermost rectrix, 31.79 ± .40 (σ, 4.71); tail spot/tail ratio, 35.59 ± .45 (σ, 5.17). (See Table 5.)

Average dimensions of females. Wing, 83.45 ± .42 (σ, 2.31); tail, 90.43 ± .02 (σ, 3.37); culmen, 15.20 ± .10 (σ, 0.55); width of lower mandible, 8.79 ± .07 (σ, 0.36); tarsus, 27.91 ± .20 (σ, 1.03); middle toe without claw, 19.66 ± .16 (σ, 0.85); length of white on inner web of outermost rectrix, 26.98 ± .70 (σ, 3.64); tail spot/tail ratio, 29.41 ± .74 (σ, 3.87). (See Table 6.)

Average color of males. Back, Olivaceous Black (3); flanks, 13-D-11; breast, Olivaceous Black (3); top of head, Olivaceous Black (3).

Table 5
P. e. canaster
Males

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	145	87.30	.21	2.50	84.81–89.80	78.0– 93.0
Tail	136	94.95	.30	3.53	91.42–98.48	86.0–105.0
Tail Spot	136	31.79	.40	4.71	27.08–36.51	18.0– 43.6
Culmen	142	15.44	.05	.50	14.85–16.04	14.5– 17.0
Mandible Width	141	8.94	.03	.37	8.57– 9.30	8.2– 9.7
Tarsus	145	28.19	.08	1.00	27.19–29.19	25.2– 31.0
Middle Toe	145	20.19	.07	.88	19.31–21.07	18.0– 22.5
Tail Spot/Tail	130	35.59	.45	5.17	27.42–37.76	19.0– 45.0

Average color of females. Back, 15-E-7; flanks, 13-K-9; breast, 15-C-12; top of head, 7-A-12.

Iris color. Variable, red to pale orange, occasionally yellow. (See Table 21.)

Breeding range. From eastern Louisiana (Iberia, Pointe Coupee, and West Carroll Parishes), and western Mississippi (Bolivar County),

Table 6
P. e. canaster
Females

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	31	83.45	.42	2.31	81.14–85.76	79.5–87.0
Tail	27	90.43	.62	3.37	87.06–93.80	83.5–96.0
Tail Spot	25	26.98	.70	3.64	23.35–30.62	18.8–35.6
Culmen	27	15.20	.10	.55	14.67–15.75	14.0–16.5
Mandible Width	28	8.79	.07	.36	8.43– 9.16	8.2– 9.4
Tarsus	27	27.91	.20	1.03	26.88–28.94	25.6–29.5
Middle Toe	27	19.66	.16	.85	18.82–20.51	17.6–21.0
Tail Spot/Tail	27	29.41	.74	3.87	25.54–33.27	22.0–39.0

north to southern Tennessee (Shelby and Wayne Counties), northern Alabama (Colbert, Limestone, Shelby, and Calhoun Counties), and central Georgia (Chattooga, Floyd, Paulding, Cobb, Gwinnett, Jackson, Clarke, and Oglethorpe Counties to Taliaferro, Hancock, Putman, Jasper, Lamar, and Merriwether Counties), south to middle eastern Alabama (Russell and Montgomery Counties), thence south to the Gulf Coast, in western Florida (Okaloosa and Santa Rosa Counties), southern Alabama, Mississippi, and southeastern Louisiana (St. Bernard, Assumption, and Iberia Parishes). Also in central-southern North Carolina (Richmond County). (See Map 2.)

Winter range. From southeastern Louisiana, central Mississippi (Warren County), central Alabama (Jefferson County), and northern Georgia (Rabun County), to coastal South Carolina (Beaufort, Charleston, and Georgetown Counties) and eastern North Carolina (Pitt County), south to southern Georgia (Toombs, Lowndes, and Brooks Counties), to western Florida (Wakulla and Leon Counties), and thence westward along the Gulf to southeastern Louisiana. (See Map 3.)

Comments. The habitat preference of this form as noted near the type locality is apparently slightly different from that of *P. e. alleni* or *P. e. rileyi*. Exploration of what appeared to me to be suitable habitats, on the basis of my own experience in Florida, produced not a single towhee. Specimens taken near Mobile, Alabama, came from extremely dense hammock-like habitats.

This form is not completely sedentary in its habits, but on the other hand it does not move as far south in winter as do *erythrophthalmus* and *rileyi*.

Specimens Examined

Atypical specimens are indicated as follows:

* *canaster* > *rileyi*
** *canaster* > *erythrophthalmus*

Breeding males. ALABAMA: Baldwin Co., 1 (UMMZ); Calhoun Co., 2 (USNM); Colbert Co., 3 (USNM); Limestone Co., 3 (USNM); Mobile Co., 4 (USNM), 2 (JCD), 1 (LSU); Russell Co., 1 (USNM); Shelby Co., 2 (USNM). FLORIDA: Okaloosa Co., 3* (CM), 1 (JCD); Santa Rosa Co., 1 (JCD), 1 (USNM). GEORGIA: Carroll Co., 1 (USNM); Chatooga Co., 2 (USNM); Clarke Co., 2 (LSU), 1 (MMP), 9 (USNM), 1** (USNM), 2* (USNM); Clayton Co., 2 (USNM); Cobb Co., 1 (USNM), 1* (USNM); DeKalb Co., 2 (LSU), 1* (MMP), 4 (USNM); Douglas Co., 1 (USNM); Floyd Co., 2 (USNM); Fulton Co., 2 (MMP), 2 (USNM), 1** (USNM); Gwinnett Co., 2 (USNM); Hancock Co., 1 (USNM); Haralson Co., 1 (USNM); Henry Co., 1 (USNM), 1* (USNM); Jackson Co., 3 (USNM); Jasper Co., 1 (USNM); Lamar Co., 1* (USNM); Meriweather Co., 1 (USNM); Morgan Co., 1 (USNM); Oglethorpe Co., 1 (USNM); Paulding Co., 2 (USNM); Putnam Co., 1 (USNM); Rockdale Co., 1 (USNM); Taliaferro Co., 2 (USNM); Walton Co., 1 (USNM.) LOUISIANA: Assumption Parish, 1 (LSU), East Baton Rouge Parish, 2 (LSU), 5 (USNM); Iberia Parish, 1 (MMP); Orleans Parish, 7 (USNM), 6 (LSU), 1 (MMP); Pointe Coupee Parish, 1 (GMS); Saint Bernard Parish, 2 (USNM); West Baton Rouge Parish, 1 (CHAM); West Carroll Parish, 1 (LSU); West Feliciana Parish, 1 (USNM). MISSISSIPPI: Adams Co., 2 (USNM); Bolivar Co., 1 (USNM), 1 (CNHM); Hancock Co., 1 (USNM); Harrison Co., 4 (LSU), 11 (USNM); Warren Co., 1 (USNM). TENNESSEE: Shelby Co., 3 (LSU); Wayne Co., 3 (USNM).

Breeding Females. ALABAMA: Calhoun Co., 1 (USNM); Mobile Co., 1 (USNM), 1 (JCD); Russell Co., 1 (USNM). FLORIDA: Okaloosa Co., 1 (CM). GEORGIA: Clarke Co., 2 (MMP), 1 (USNM); Cobb Co., 1 (CNHM), 2 (USNM); DeKalb Co., 2 (USNM); Fayette Co., 1 (USNM); Fulton Co., 1 (MMP), 2 (USNM); Hancock Co., 1 (USNM); Oglethorpe Co., 1 (USNM); Taliaferro Co., 1 (USNM). LOUISIANA: East Baton Rouge Parish, 1 (USNM); Orleans Parish, 1 (USNM); Pointe Coupee Parish, 1 (GMS). MISSISSIPPI: Bolivar Co., 1 (CNHM); Harrison Co., 3 (USNM); Pearl River Co., 1 (AMNH). NORTH CAROLINA: Richmond Co., 1 (USNM).

Wintering Males. ALABAMA: Baldwin Co., 1 (USNM); Jefferson Co., 1 (LSU); Lee Co., 1 (USNM); Mobile Co., 1 (LSU). FLORIDA:

Leon Co., 1 (CNHM); Okaloosa Co., 3 (CM); Santa Rosa Co., 2 (CNHM);Wakulla Co., 1 (USNM). GEORGIA: Barrow Co., 1 (USNM); Brooks Co., 1 (USNM); Clarke Co., 6 (USNM); DeKalb Co., 2 (USNM), 1 (DZUG); Fulton Co., 2 (USNM); Lowndes Co., 1 (USNM); Madison Co., 2 (USNM); Oconee Co., 2 (USNM); Walton Co., 1 (USNM). LOUISIANA: East Baton Rouge Parish, 3 (LSU), 1 (USNM); Orleans Parish, 3 (LSU), 2 (CNHM). MISSISSIPPI: Amite Co., 1 (USNM); Forrest Co., 1 (LSU); Harrison Co., 1 (LSU), 6 (USNM); Rankin Co., 1 (MMP); Warren Co., 1 (LSU). NORTH CAROLINA: Pitt Co., 1 (USNM). SOUTH CAROLINA: Beaufort Co., 1 (CHAM), 1 (MCZ).

Wintering Females. ALABAMA: Houston Co., 4 (USNM); Orange Beach, 1 (USNM). FLORIDA: Escambia Co., 1 (USNM); Leon Co., 1* (CNHM); Okaloosa Co., 1 (CM); Santa Rosa Co., 1 (CNHM); 1* (CNHM); Wakulla Co., 1 (FSM), 1* (USNM). GEORGIA: Cobb Co., 1 (CNHM), 1* (CNHM); DeKalb Co., 1 (USNM); Rabun Co., 1 (USNM). LOUISIANA: East Baton Rouge Parish, 1 (CNHM), 1 (LSU), 1 (USNM); Orleans Parish, 1 (LSU), 2 (USNM); Chef Menteur, 1 (CNHM). MISSISSIPPI: Harrison Co., 4 (LSU), 1 (USNM); Rankin Co., 1 (MMP). SOUTH CAROLINA: Charleston Co., 1 (CHAM); Georgetown Co., 1* (USNM).

Migrant Males. ALABAMA: Baldwin Co., 2* (USNM); Mobile Co., 1* (USNM); FLORIDA: Escambia Co., 1 (USNM); Okaloosa Co., 1 (CM). GEORGIA: Clarke Co., 2 (USNM); Cobb Co., 2 (CNHM); DeKalb Co., 1 (USNM); Harris Co., 1 (USNM); Jefferson Co., 1 (USNM); Toombes Co., 1 (USNM); Treutlen Co., 1 (USNM); Washington Co., 1 (USNM). LOUISIANA: East Baton Rouge Parish, 1 (LSU), 2 (USNM); Orleans Parish, 2 (LSU); West Feliciana Parish, 1 (GMS). MISSISSIPPI: Harrison Co., 1 (USNM), 2* (USNM), 1 (MMP); Pearl River Co., 1 (AMNH); Warren Co., 2 (CNHM). NORTH CAROLINA: Carteret Co., 1* (USNM). SOUTH CAROLINA: Georgetown Co., 1 (USNM). TENNESSEE: Roane Co., 1 (USNM).

Migrant Females. GEORGIA: Clarke Co., 1 (MMP); Harris Co., 1 (USNM). LOUISIANA: East Baton Rouge Parish, 1 (USNM); Orleans Parish, 1 (LSU). MISSISSIPPI: Harrison Co., 2 (USNM).

Pipilo erythrophthalmus rileyi Koelz

Pipilo leucopis Maynard (1878: 113, pl. IV), part.

Pipilo erythrophthalmus var. *alleni*, Baird, Brewer, and Ridgway (1874: 112), part.

Pipilo alleni Koelz (1939: 121), original description. Type locality: Brunswick, Georgia.

Description

Diagnosis. A medium-sized, large-billed race, with variable eye color, and showing less white on the rectrices than its northern relatives.

Average dimensions of males. Wing, 85.53 ± .26 (σ, 2.62); tail, 94.59 ± .36 (σ, 3.43); culmen, 15.64 ± .62 (σ, 0.62); width of lower mandible, 8.85 ± .03 (σ, 0.31); tarsus, 28.25 ± .10 (σ, 0.99); middle toe without claw, 19.89 ± .07 (σ, 0.68); length of white on inner web of outermost rectrix, 25.50 ± .41 (σ, 3.72). (See Table 7.)

Average dimensions of females. Wing, 80.32 ± .46 (σ, 2.81); tail 89.70 ± .67 (σ, 3.67); exposed culmen, 15.34 ± .09 (σ, 0.53); width of lower mandible, 8.69 ± .05 (σ, 0.27); tarsus, 27.54 ± .19 (σ, 1.15); middle toe without claw, 19.38 ± .11 (σ, 0.67); length of white on inner web of outermost rectrix, 22.85 ± .61 (σ, 2.93). (See Table 8.)

Average color of males. Back, Olivaceous Black; flanks, 13-D-11; breast, Olivaceous Black; top of head, Olivaceous Black.

Average color of females. Back, 15-C-11; flanks, 13-K-11; breast, 15-C-9; top of head, 8-H-11.

Table 7
P. c. rileyi
Males

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	100	85.54	.26	2.62	82.91–88.15	80.0– 92.0
Tail	91	94.59	.36	3.43	91.16–93.03	87.0–103.0
Tail Spot	84	25.50	.41	3.71	21.78–29.22	17.0– 34.0
Culmen	98	15.64	.06	.62	15.01–16.26	14.1– 17.0
Mandible Width	96	8.85	.03	.31	8.54– 9.16	8.0– 9.5
Tarsus	100	28.25	.10	.99	27.26–29.24	25.3– 30.6
Middle Toe	100	19.89	.07	.68	19.21–20.57	17.0– 21.5

Iris color. Variable, straw to orange or red. (See Table 21).

Breeding range. From western Florida (Walton County), southeastern Alabama (Houston County), northeast through southeastern Georgia (Early, Dougherty, Crisp, Jones, Warren, McDuffie and Richmond Counties) to coastal South Carolina (Jasper, Beaufort, Charleston, and Georgetown Counties) and coastal North Carolina (Brunswick, New Hanover and Carteret Counties) south along the coast of

Table 8
P. e. rileyi
Females

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	38	80.32	.46	2.81	77.51–83.13	72.5–85.0
Tail	30	89.70	.67	3.66	86.04–93.36	80.9–97.0
Tail Spot	23	22.84	.61	2.93	19.92–25.78	19.9–30.3
Culmen	38	15.34	.09	.53	14.81–15.87	14.5–16.5
Mandible Width	37	8.69	.05	.27	8.42– 8.96	8.2– 9.4
Tarsus	36	27.54	.19	1.15	26.39–28.69	25.4–29.6
Middle Toe	38	19.38	.11	.67	18.71–20.06	17.5–20.5

Georgia (Chatham, Glynn and Camden Counties) thence west through southern Georgia (Charlton County) and northern Florida (Madison and Leon Counties) to the Gulf Coast (Wakulla County). (See Map 2.)

Winter range. From western Florida (Escambia County), eastern Alabama (Lee County) north to north-central Georgia (Cobb, Walton and Clarke Counties) to coastal South Carolina (Beaufort, Jasper, Dorchester, Charleston and Georgetown Counties) and eastern North Carolina (Robeson, Carteret, Pitt and Hyde Counties) south to mid-peninsular Florida (Brevard, Charlotte and Pinellas Counties). (See Map 3.)

Comments. This pale-eyed race is clearly distinguished from *P. e. alleni* by its larger wing and greater amount of white on the rectrices. It can be distinguished from *P. e. erythrophthalmus* and *P. e. canaster* by the color of its irides and by the intermediate amount of white present on the rectrices. The color of the flanks in *rileyi*, especially in the males, is remarkably uniform in the material examined and is much darker than that found in *P. e. alleni*.

My experience with this race at the type locality during the breeding season agrees with that of Walter Koelz, the original describer. The preferred habitat is in scrubby, moderately dense growth. Specimens were taken on St. Simons Island, and on the mainland a few miles to the north and south of Brunswick, Georgia, in much the same type of habitat that is preferred by *P. e. alleni* in Florida. Material from west Florida, in Walton County, was also taken in this same scrub association.

Specimens Examined

Atypical specimens are indicated as follows:

* *rileyi* > *canaster*
** *rileyi* > *erythrophthalmus*
*** *rileyi* > *alleni*

Breeding Males. ALABAMA: Houston Co., 1 (USNM). FLORIDA: Leon Co., 4 (USNM); Madison Co., 1 (USNM); Walton Co., 6 (JCD), 1* (JCD), 1 (AMNH). SOUTH CAROLINA: Beaufort Co., 1 (MCZ), 1 (AMNH), 1 (USNM); Charleston Co., 1 (CHAM), 1** (CHAM), 3 (MCZ), 1* (MCZ), 2 (USNM); Georgetown Co., 1 (USNM), 1* (USNM); Jasper Co., 1 (USNM). NORTH CAROLINA: Brunswick Co., 2** (NCS); Carteret Co., 1 (NCS); New Hanover Co., 1 (USNM), 1* (USNM). GEORGIA: Baker Co., 3 (DZUG), 2 (USNM); Ben Hill Co., 1 (USNM); Bibb Co., 1 (USNM); Bullock Co., 1 (USNM); Burke Co., 1 (USNM), 1* (USNM); Camden Co., 1 (DZUG), 1 (MCZ); Candler Co., 1 (USNM); Charlton Co., 1 (DZUG), 1 (USNM); Chatham Co., 1 (CHAM), 3 (USNM); Coffee Co., 1 (USNM); Colquitt Co., 1 (USNM); Cook Co., 1 (USNM); Crisp Co., 2 (USNM); Decatur Co., 1 (DZUG); Dodge Co., 1 (USNM); Dougherty Co., 1* (USNM), 1 (DZUG); Early Co., 1 (DZUG); Effingham Co., 1 (USNM); Glynn Co., 7 (JCD), 1 (PB), 1 (DZUG); Grady Co., 1*** (USNM); Irwin Co., 1 (USNM); Jones Co., 1 (LSU), 2 (USNM); Lowndes Co., 1 (USNM); Macduffie Co., 1 (MMP); Pierce Co., 1 (USNM); Pulaski Co., 1 (USNM); Richmond Co., 1 (MMP), 3 (USNM); Thomas Co., 2 (USNM), 1* (USNM); Turner Co., 1 (USNM); Ware Co., 2 (USNM); Warren Co., 1* (USNM).

Breeding Females. FLORIDA: Franklin Co., 1 (USNM); Leon Co., 1* (USNM); Walton Co., 5 (JCD), 1* (USNM). GEORGIA: Bacon Co., 1 (USNM); Baker Co., 1 (DZUG), 1 (USNM); Ben Hill Co., 1 (USNM); Brantly Co., 1 (DZUG); Candler Co., 1 (USNM); Chatham Co., 1 (USNM); Colquitt Co., 1 (USNM); Cook Co., 1 (USNM); Crisp Co., 1 (USNM); Decatur Co., 1 (DZUG); Dodge Co., 1 (USNM) Dougherty Co., 2 (DZUG); Glynn Co., 3 (JCD), 1 (PB); Grady Co., 1 (USNM); McDuffie Co., 1 (USNM); Sumter Co., 1 (MMP); Ware Co., 1 (USNM). NORTH CAROLINA; Brunswick Co., 1 (USNM); Carteret Co., 1 (USNM). SOUTH CAROLINA: Charleston Co., 1 (MCZ), 1** (MCZ), 2 (USNM); Georgetown Co., 1 (USNM).

Wintering Males. ALABAMA: Lee Co., 2 (UMMZ). FLORIDA: Alachua Co., 1 (AMNH); Baker Co., 1 (USNM); Brevard Co., 2 (CNHM); Charlotte Co., 1 (MCZ); Columbia Co., 1 (LSU); Duval Co., 1 (USNM); Escambia Co., 1 (LSU), 1 (USNM); Franklin Co.,

2 (LSU), 1 (USNM); Hamilton Co., 1 (USNM); Levy Co., 4 (AMNH); Nassau Co., 2 (AMNH); Okaloosa Co., 9 (CM); Pinellas Co., 1 (AMNH); Putnam Co., 1 (CNHM); Santa Rosa Co., 12 (CNHM); Walton Co., 1 (USNM). GEORGIA: Berrien Co., 1 (USNM); Calhoun Co., 1 (USNM); Camden Co., 1 (DZUG), 2 (MCZ), 5 (AMNH); Charlton Co., 3 (USNM); Chatham Co., 2 (USNM), 4 (CHAM); Clarke Co., 1 (USNM); Echols Co., 1 (DZUG), 1 (USNM); Glynn Co., 1 (LSU), 1 (MMP), 1 (UMMZ); Liberty Co., 1 (USNM); McIntosh Co., 2 (AMNH); Tatnall Co., 1 (USNM); Walton Co., 1 (USNM). NORTH CAROLINA: Carteret Co., 3 (USNM); Pitt Co., 2 (USNM). SOUTH CAROLINA: Beaufort Co., 5 (MCZ), 2 (USNM), 1 (AMNH); Charleston Co., 6 (CHAM), 2 (USNM); Georgetown Co., 1 (USNM).

Wintering Females. FLORIDA: Alachua Co., 1 (CNHM), 1 (USNM); Brevard Co., 1 (MCZ); Escambia Co., 1 (LSU), 1 (USNM); Levy Co., 1 (AMNH); Nassau Co., 1 (CNHM); Okaloosa Co., 7 (CM); Columbia Co., 1 (LSU); Pinellas Co., 1 (CNHM); Santa Rosa Co., 9 (CNHM); Volusia Co., 1 (MCZ); Wakulla Co., 1 (FSM), 1 (USNM); Walton Co., 1 (USNM). GEORGIA: Berrien Co., 1 (USNM); Brooks Co., 1 (USNM); Camden Co., 1 (MCZ); Chatham Co., 2 (CHAM); Clarke Co., 2 (USNM); Echols Co., 1 (DZUG); Glynn Co., 1 (LSU), 1 (MMP), 1 (UMMZ); Hinesville, 1 (USNM). NORTH CAROLINA: Carteret Co., 2 (USNM); Hyde Co., 1 (USNM); Robeson Co., 1 (CNHM). SOUTH CAROLINA: Charleston Co., 3 (CHAM); Dorchester Co., 1 (CHAM); Georgetown Co., 1 (USNM); Jasper Co., 2 (USNM).

Migrant Males. FLORIDA: Levy Co., 1 (AMNH); Okaloosa Co., 1 (CM); Santa Rosa Co., 1 (USNM), 2 (CNHM). GEORGIA: Bryan Co., 1 (USNM); Camden Co., 1 (USNM); Chatham Co., 1 (MCZ); Cobb Co., 1 (CNHM); Cook Co., 1 (MMP); Decatur Co., 1 (DZUG); Evans Co., 1 (USNM); Liberty Co., 2 (USNM); Long Co., 1 (USNM); McIntosh Co., 1 (UMMZ); Tatnall Co., 1 (DZUG), 1 (USNM); Telfair Co., 1 (USNM); Thomas Co., 1 (AMNH); Washington Co., 1 (USNM). NORTH CAROLINA: Pitt Co., 1* (USNM). SOUTH CAROLINA: Charleston Co., 1 (CNHM), 3 (MCZ); Georgetown Co., 1 (USNM).

Migrant Females. FLORIDA: Escambia Co., 2 (USNM); Franklin Co., 1 (JCD); Okaloosa Co., 1 (CM); Santa Rosa Co., 2 (CNHM), 1 (USNM). GEORGIA: Camden Co., 2 (MCZ), 1 (USNM); Cook Co., 1 (MMP); Fulton Co., 1 (USNM); Tatnall Co., 1 (USNM); Treutlen Co., 1 (USNM). SOUTH CAROLINA: Beaufort Co., 1 (MCZ), Charleston Co., 1 (MCZ), 2 (USNM); Georgetown Co., 1* (USNM); Greenville Co., 1* (USNM).

GEOGRAPHIC VARIATION

Following preliminary examination, the material at hand was separated into six samples (Map 1). Mean, standard error of the mean, and standard deviation of the mean were calculated for each of the mensural characters investigated. These samples were treated separately for each sex, except for samples 1, 2 and 3, of which only the males were considered (Tables 9, 10 and 11). For each sex samples 1, 2 and 3 were later treated as a single sample, representing the northern population, *P. c. erythrophthalmus*. For greater clarity, these three northern samples are referred to in the following discussion as eastern, central and western, respectively. Sample 4 represents *P. c. canaster*, 5 represents *P. c. rileyi*, and 6 represents *P. c. alleni*.

Means were regarded as being significantly different when two standard errors on either side of the means did not overlap in the samples under consideration. A character was assumed to be of diagnostic value if it furnished more than 75 per cent correct separation of mixed samples.

The degrees of separation furnished by the various characters are presented in Tables 12–19. In these tables, the distance in standard units to the point of intersection of the standard distributions is represented by d/σ. *Per cent separation* is the measure of area of the standard curves which lie to either side of the point of intersection of these curves. *Division point* is the theoretical point of maximum separation in millimeters for each of the characters indicated. X indicates that the difference is not statistically significant, and Z indicates that the degree of separation accomplished by the character is less than 50.0 per cent.

Figures 1–15 present this same information in the form of Hubbs-Perlmutter diagrams. For a discussion of the use of this method of demonstrating differences between populations see Hubbs and Perlmutter (1942). In each diagram a vertical line marks the mean; a rectangle to either side indicates one standard deviation; the black part of each rectangle indicates twice the standard error of the mean; a solid line shows the observed range of variation; a broken line shows the limits of three standard deviations to either side of the mean, beyond observed range.

Wing Length

Males (Figure 1). Among the four races here recognized, *erythrophthalmus* has the longest wing, 87.57 ± .15 mm. This form represents the northern part of the range of the species and extends from the eastern seaboard to the junction with *Pipilo arcticus maculatus* on the

west. It shows a gradual increase in wing length from east to west. The eastern sample shows a mean wing length of 86.63 ± .16 mm., the central sample 87.32 ± .28 mm., and the western sample 89.77 ± .28 mm. The difference in the means of the eastern and central samples is not statistically significant.

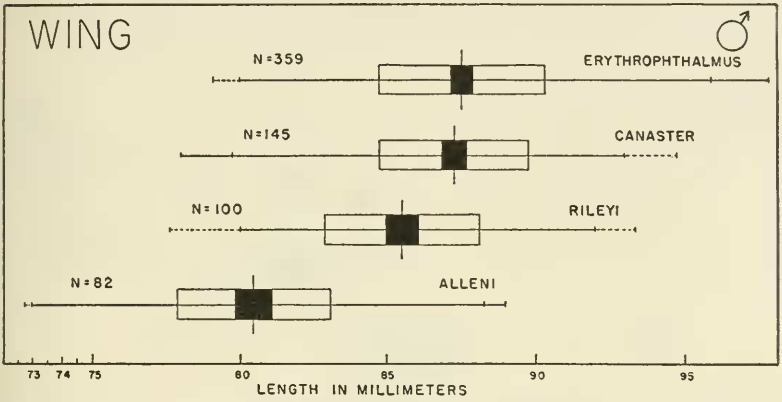

Figure 1. Variation in wing length of males. See page 304 for explanation of figure.

The western sample is significantly different from both the eastern and central samples. Ridgway (1901: 424) comments on variation within this race. He states that birds "from opposite sides of the Alleghenies differ but slightly in average measurements." He gives as substantiating evidence, measurements of 9 adult males from "east of the Alleghenies" — wing 89.92, "8 adult males from Mississippi valley" — wing 89.15. In this connection it is pertinent to note that the present study shows considerable difference in samples taken from the extreme eastern and western portions of the range of this race — enough to allow 75 per cent of the western birds to be distinguished from the eastern birds. This character, however, is of no diagnostic value in separating the central population from either the eastern or western samples.

The wing of *canaster* is not significantly shorter than that of *erythrophthalmus*. The mean length for the wing of *canaster* is 87.30 ± .21 mm.

Rileyi is significantly shorter in wing length than either *canaster* or *erythrophthalmus*. The mean length for the wing is 85.53 ± .26 mm. The difference, however, is not of such magnitude as to allow its use as a diagnostic character.

The wing of *alleni* is much shorter, averaging 80.47 ± .29 mm. Wing length is of value diagnostically, furnishing the following percentages of separation[1] from the various races: from *rileyi*, 83.5 per cent; from *erythrophthalmus*, 91 per cent; and from *canaster*, 91.5 per cent.

The general trend in the variation of wing length is from northwest to southeast, with maximum length occurring in the northwest. The most abrupt change occurs at the junction of *rileyi* and *alleni*.

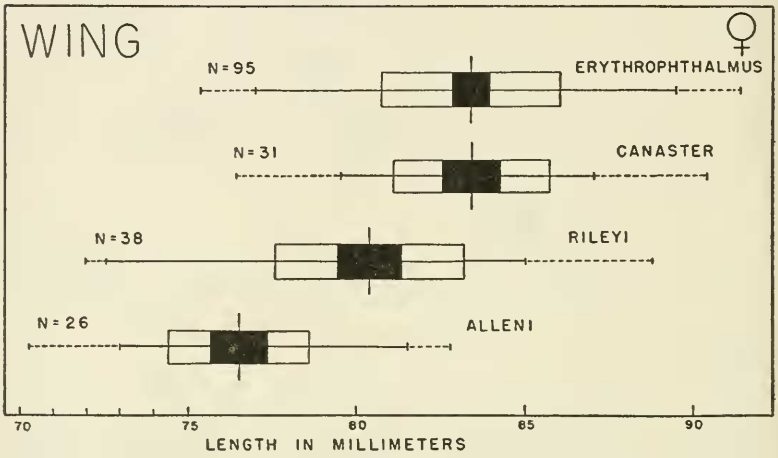

Figure 2. Variation in wing length of females. See page 304 for explanation of figure.

Females (Figure 2). The same pattern of variation observed in the males appears in the females. *Erythrophthalmus* and *canaster* have the longest wings, averaging 83.38 ± .28 and 83.45 ± .42 mm., respectively. The means are not significantly different. The wing in *rileyi* is shorter, 80.32 ± .46 mm., and furnishes 74.8 per cent separation from *canaster*, and 65.7 per cent from *erythrophthalmus*. *Alleni* has the shortest wing, 76.50 ± .47 mm. Separation of 91 per cent from *erythrophthalmus*, 94.2 per cent from *canaster* and 78.3 per cent from *rileyi* is obtained by using this character.

[1] In comparing the degree of separation of two samples the "per cent separation" was determined by averaging the separate degrees of separation afforded. Thus, if 76 per cent of Form A was separable from 74 per cent of Form B, the "per cent separation" was 75 per cent.

Table 9
P. e. erythrophthalmus
(Sample 1)
Males

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	211	86.63	.16	2.37	84.26–89.00	80.0– 94.0
Tail	205	92.04	.27	3.83	88.21–95.87	83.0–103.1
Tail Spot	200	36.10	.32	4.58	31.52–40.68	24.0– 55.0
Culmen	206	14.51	.04	.61	13.90–15.13	13.0– 16.0
Mandible Width	201	8.61	.02	.31	8.30– 8.92	7.5– 9.5
Tarsus	208	27.42	.06	.87	26.56–28.29	25.4– 29.5
Middle Toe	205	19.58	.05	.72	18.86–20.30	17.5– 22.0

Table 10
P. e. erythrophthalmus
(Sample 2)
Males

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	63	87.32	.28	2.21	85.12–89.53	82.1– 93.1
Tail	63	92.70	.43	3.42	89.28–96.11	85.9–103.0
Tail Spot	62	36.85	.61	4.79	32.07–41.64	25.1– 50.2
Culmen	62	14.56	.06	.45	14.11–15.00	13.6– 15.5
Mandible Width	63	8.61	.03	.22	8.39– 8.83	8.1– 9.2
Tarsus	58	27.05	.09	.76	26.29–27.82	24.8– 29.1
Middle Toe	63	19.64	.08	.63	19.01–20.27	18.1– 21.1

Table 11
P. e. erythrophthalmus
(Sample 3)
Males

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	85	89.77	.28	2.61	87.16–92.38	84.9– 96.0
Tail	83	96.78	.36	3.05	93.73–99.83	89.1–104.0
Tail Spot	83	38.10	.42	3.82	34.28–41.92	29.1– 50.0
Culmen	84	14.60	.06	.53	14.06–15.13	13.0– 15.9
Mandible Width	82	8.72	.03	.29	8.43– 9.01	8.0– 9.5
Tarsus	84	27.50	.09	.81	26.69–28.30	25.2– 19.5
Middle Toe	83	19.80	.08	.72	19.08–20.51	17.4– 22.4

Table 12
Pipilo erythrophthalmus erythrophthalmus versus *P. e. alleni*, *P. e. canaster* and *P. e. rileyi*

Males	*Vs. alleni*			*Vs. canaster*			*Vs. rileyi*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	1.33	91.0	83.8	X	X	X	Z	Z	Z
Tail	Z	Z	Z	Z	Z	Z	Z	Z	Z
Tail Spot	2.09	97.1	29.0	.57	68.0	34.4	1.62	94.5	30.7
Culmen	Z	Z	Z	.81	79.0	15.0	.96	88.0	15.0
Mandible	Z	Z	Z	Z	Z	Z	Z	Z	Z
Tarsus	Z	Z	Z	Z	Z	Z	Z	Z	Z
Toe	.53	70.0	19.81	Z	Z	Z	Z	Z	Z

Table 13

Pipilo erythrophthalmus erythrophthalmus versus *P. e. canaster*, *P. e. alleni* and *P. e. rileyi*

Females	*Vs. canaster*			*Vs. alleni*			*Vs. rileyi*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	X	X	X	1.40	92.0	79.6	.53	60.0	81.9
Tail	X	X	X	Z	Z	Z	X	X	X
Tail Spot	.80	79.0	28.8	2.14	93.5	24.0	1.36	92.0	27.3
Culmen	.65	74.5	14.9	Z	Z	Z	.79	79.0	15.1
Mandible	X	X	X	X	X	X	X	X	X
Tarsus	.65	74.5	27.2	Z	Z	Z	Z	Z	Z
Toe	Z	Z	Z	X	X	X	X	X	X

Table 14

Pipilo erythrophthalmus canaster versus *P. e. alleni*, *P. e. erythrophthalmus* and *P. e. rileyi*

Males	*Vs. alleni*			*Vs. erythrophthalmus*			*Vs. rileyi*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	1.33	91.0	85.0	X	X	X	Z	Z	Z
Tail	Z	Z	Z	Z	Z	Z	X	X	X
Tail Spot	1.33	91.0	25.6	.55	71.0	34.4	.71	76.5	28.2
Culmen	Z	Z	Z	.81	79.5	15.0	X	X	X
Mandible	.68	75.0	8.7	Z	Z	Z	X	X	X
Tarsus	.72	76.5	27.5	Z	Z	Z	X	X	X
Toe	.77	78.0	19.5	Z	Z	Z	Z	Z	Z

Table 15

Pipilo erythrophthalmus canaster versus *P. e. alleni*, *P. e. rileyi* and *P. e. erythrophthalmus*

Females	*Vs. alleni*			*Vs. rileyi*			*Vs. erythrophthalmus*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	1.55	94.0	79.9	.57	75.0	82.1	X	X	X
Tail	.74	77.0	87.9	X	X	X	X	X	X
Tail Spot	1.58	94.0	21.2	.67	75.0	24.6	.76	78.0	28.8
Culmen	Z	Z	Z	X	X	X	.60	72.0	14.9
Mandible	Z	Z	Z	X	X	X	X	X	X
Tarsus	1.05	85.5	26.8	X	X	X	X	X	X
Toe	.73	77.0	19.1	X	X	X	Z	Z	Z

Table 16

Pipilo erythrophthalmus rileyi versus *P. e. alleni*, *P. e. erythrophthalmus* and *P. e. canaster*

Males	*Vs. alleni*			*Vs. erythrophthalmus*			*Vs. canaster*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	.97	83.5	83.0	Z	Z	Z	Z	Z	Z
Tail	Z	Z	Z	Z	Z	Z	X	X	X
Tail Spot	.73	77.0	23.0	1.41	92.0	30.72	.74	78.0	28.2
Culmen	Z	Z	Z	.86	80.5	15.0	X	X	X
Mandible	.60	77.5	8.7	Z	Z	Z	X	X	X
Tarsus	.75	77.5	27.5	Z	Z	Z	X	X	X
Toe	.70	76.0	19.5	Z	Z	Z	Z	Z	Z

Table 17

Pipilo erythrophthalmus rileyi versus *P. e. alleni*, *P. e. canaster* and *P. e. erythrophthalmus*

Females	*Vs. alleni*			*Vs. canaster*			*Vs. erythrophthalmus*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	.81	79.5	78.0	.65	74.5	82.1	.57	71.5	81.9
Tail	.62	73.0	87.4	X	X	X	X	X	X
Tail Spot	1.34	91.0	19.5	.59	72.0	24.6	1.53	94.0	27.3
Culmen	.64	74.0	15.0	X	X	X	.74	77.0	15.1
Mandible	Z	Z	Z	X	X	X	X	X	X
Tarsus	.83	80.0	26.6	X	X	X	Z	Z	Z
Toe	.46	67.5	19.0	X	X	X	X	X	X

Table 18

Pipilo erythrophthalmus alleni versus *P. e. rileyi*, *P. e. erythrophthalmus* and *P. e. canaster*

Males	*Vs. rileyi*			*Vs. erythrophthalmus*			*Vs. canaster*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	.97	83.5	83.0	1.31	91.0	83.8	1.35	92.0	85.0
Tail	Z	Z	Z	Z	Z	Z	Z	Z	Z
Tail Spot	.68	75.5	23.0	1.91	97.1	28.2	1.31	91.0	26.6
Culmen	Z	Z	Z	Z	Z	Z	Z	Z	Z
Mandible	.57	71.0	8.8	Z	Z	Z	.64	74.0	8.7
Tarsus	.76	78.0	27.5	Z	Z	Z	.73	77.0	27.5
Toe	.64	74.0	19.5	.46	67.5	19.3	.78	78.5	19.5

Table 19

Pipilo erythrophthalmus alleni versus *P. e. rileyi*, *P. e. canaster* and *P. e. erythrophthalmus*

Females	*Vs. rileyi*			*Vs. canaster*			*Vs. erythrophthalmus*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	.74	77.0	78.0	1.62	94.5	79.9	1.51	93.5	79.6
Tail	.59	75.5	87.4	.74	77.0	87.9	Z	Z	Z
Tail Spot	1.26	87.5	19.5	1.60	94.5	21.2	2.39	99.2	24.0
Culmen	.61	73.0	15.0	.40	66.5	14.9	Z	Z	Z
Mandible	Z	Z	Z	Z	Z	Z	X	X	X
Tarsus	.84	80.0	26.6	1.06	85.5	26.8	Z	Z	Z
Toe	.60	77.5	19.0	.68	75.5	19.1	X	X	X

Tail Length

Males (Figure 3). *Canaster* and *rileyi* have the longest tails. *Canaster* averages 94.95 ± .30 mm. and *rileyi* 94.59 ± .36 mm. They are not significantly different in this respect. Both *canaster* and *rileyi* differ

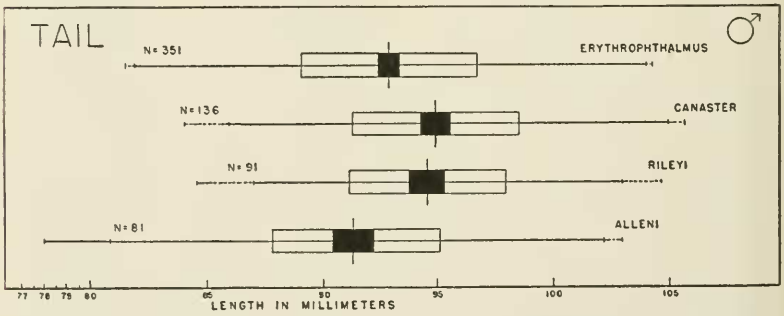

Figure 3. Variation in tail length of males. See page 304 for explanation of figure.

significantly from *erythrophthalmus* and *alleni*. *Erythrophthalmus* has a mean tail length of 92.91 ± .20 and *alleni* 91.43 ± .42 mm.

The trend of geographic variation in wing length within *P. e. erythrophthalmus* is repeated in tail length. The three samples from east to west average respectively, 92.04 ± .27, 92.70 ± .44 and 96.78 ± .36 mm. The western sample is again significantly different from the other two. Ridgway's measurements show the reverse in so far as general trend — nine eastern males 94.74, eight western males 93.73 mm.

Tail length, while of no value as a diagnostic character, shows an interesting pattern of geographic variation: maximum length in the far northwest, next largest in the coastal plains and piedmont areas, smaller again in the north-central and eastern areas, and smallest in peninsular Florida.

Females (Figure 4). *Canaster* and *rileyi* have the longest tails, the former averaging 90.43 ± .62 mm., and the latter 89.70 ± .67 mm. The difference is not statistically significant. The tail in *erythrophthalmus* is not significantly shorter than these, averaging 88.22 ± .41 mm. *Alleni* has a much shorter tail, 85.43 ± .67 mm., and this charac-

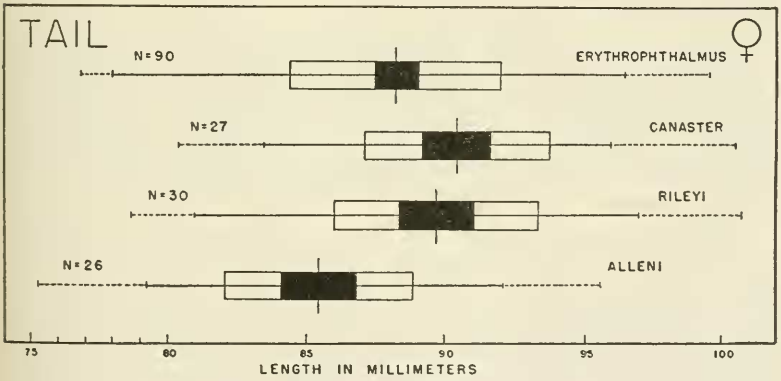

Figure 4. Variation in tail length of females. See page 304 for explanation of figure.

ter serves to separate the Florida race from *rileyi* and *canaster*, with 74.3 per cent and 77 per cent accuracy, respectively. The mean tail length in *alleni*, though significantly different from that of *erythrophthalmus*, furnishes less than 50 per cent separation from this form.

Tail Spot

Males (Figure 5). *Erythrophthalmus* shows the greatest linear extent of white on the outermost rectrix, 36.70 ± .24 mm. The western

sample of this population averages 38.10 ± .15 mm., a significant difference from the eastern (36.10 ± .32) but not from the central sample (36.85 ± .61 mm.). Ridgway, in commenting on variation in this character in *P. e. erythrophthalmus*, found the reverse of the results presented here. His nine eastern males and eight western males averaged 40.64 and 38.35 mm., respectively.

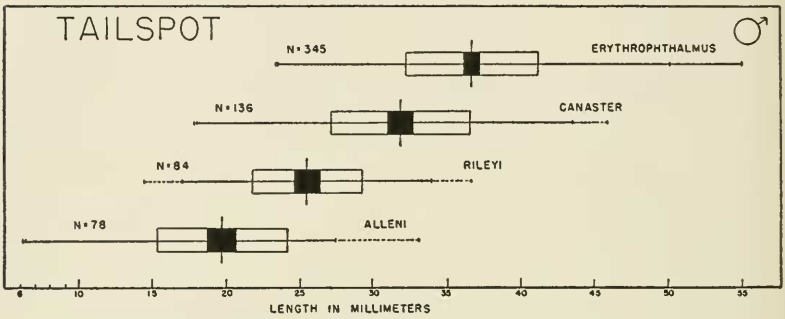

Figure 5. Variation in length of white spot on outermost rectrix of males. See page 304 for explanation of figure.

The tail spot of *canaster* averages 31.79 ± .40 mm., a significant difference from that of *erythrophthalmus*. Howell (1913) used this as a diagnostic character in separating *canaster* from *erythrophthalmus*. However, I find this to be unreliable under statistical scrutiny, since only 69.5 per cent of the *erythrophthalmus* sample is separable from that of *canaster*.

Rileyi has the next smallest amount of white on the tail, averaging 25.50 ± .41 mm. This race shows a significant difference from *erythrophthalmus*, *canaster* and *alleni*. In my samples *rileyi* shows 77.3 per cent separation from *canaster*, 93.3 per cent from *erythrophthalmus*, and 76.3 per cent from *alleni*. This character is of diagnostic value in separating *rileyi* from *canaster*, *erythrophthalmus* and *alleni*.

P. e. alleni has the smallest amount of white on the tail, the spot on the outermost rectrix averaging 19.71 ± .50 mm. The difference is statistically significant and allows the use of this measurement for diagnostic purposes. The tail spot of *alleni* affords 97.1 per cent separation from *erythrophthalmus*, 76.3 per cent from *rileyi*, and 90.8 per cent from *canaster*.

The variation in this character shows a northwest-southeast trend, the amount of white diminishing as populations are examined from North Dakota south and east to peninsular Florida. Of interest is the fact that among the Florida material studied, those having the smallest

amount of white (6–8 mm.) came from coastal localities within the peninsula.

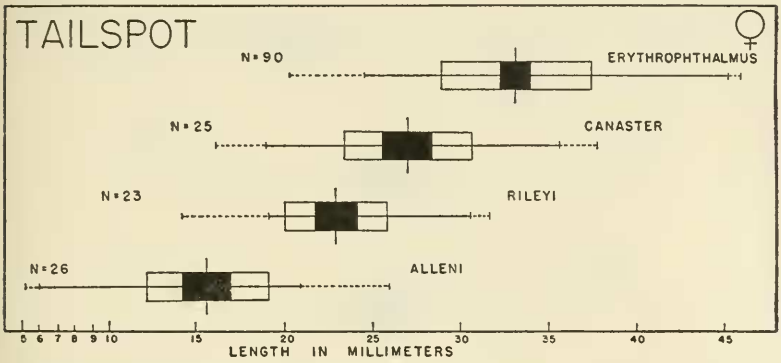

Figure 6. Variation in length of white spot on outermost rectrix of females. See page 304 for explanation of figure.

Females (Figure 6). *P. e. erythrophthalmus* shows the greatest amount of white on the rectrices. The average extent is 33.18 ± .46. This character is of diagnostic value in separating *erythrophthalmus* from *canaster* (78.5 per cent), from *rileyi* (93.0 per cent) and from *alleni* (94.3 per cent). *Canaster* in turn is separable from *rileyi* (73.5 per cent) and from *alleni* (94.3 per cent). *Rileyi-alleni* separation on the basis of this character is 89.3 per cent correct. The females show the same pattern of geographic variation as do the males.

Culmen Length

Males (Figure 7). The length of culmen is quite different in its geographical variation from those characters previously discussed. Howell (1913: 202) first called attention to the longer bill found in the race he designated as *canaster*. In the material examined in this study it was found that the culmen of *canaster* averages 15.44 ± .05 mm. *Erythrophthalmus*, to the north, averages 14.49 ± .03 mm. On the basis of this character 75.3 per cent separation of *erythrophthalmus* from *canaster* obtains.[1]

In the three northern samples (*erythrophthalmus*) no significant difference in culmen length was found. The eastern segment of the

[1] From a practical standpoint it is unfortunate that the optimum point of division falls at 14.96 mm. The culmen measurement is at best a difficult one to make on a short-, heavy-billed bird such as the towhee. In addition the fact that this point lies near an even millimeter, possibly causing bias in measurement, is not helpful. This does not negate the difference, however, and the culmen length is certainly an indicator of the racial distinctness of this form.

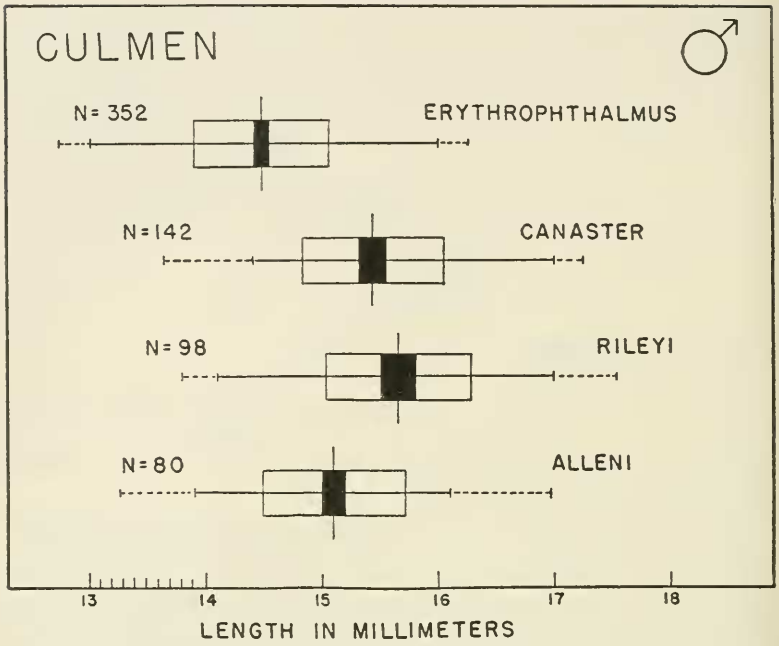

Figure 7. Variation in culmen length of males. See page 304 for explanation of figure.

population averaged 14.51 ± .04, the central segment 14.56 ± .06 and the western segment 14.60 ± .06 mm. Ridgway found a greater difference in the material he had at hand, nine eastern males averaging 14.22 and eight western males averaging 13.97 mm.

The culmen of *rileyi* is significantly longer than that of *canaster*, averaging 15.65 ± .06 mm. The difference is not sufficient to separate *canaster* from *rileyi*. However, 84.3 per cent of *rileyi* and *erythrophthalmus* are separable.

Culmen length in *alleni* is significantly less than that of *canaster* and *rileyi*, the average length being 15.05 ± .07 mm. Although serving to indicate a difference in the population, it is not of diagnostic value.

Maximum culmen length is obtained in *canaster* and *rileyi*. To the north and south it diminishes, and the northwest-southeast trend is not as pronounced as in other characters.

Females (Figure 8). *P. e. canaster* and *rileyi* females have the longest culmens, averaging 15.20 ± .10 mm. and 15.34 ± .09 mm., respectively. *Canaster* is separable with 73.5 per cent accuracy from

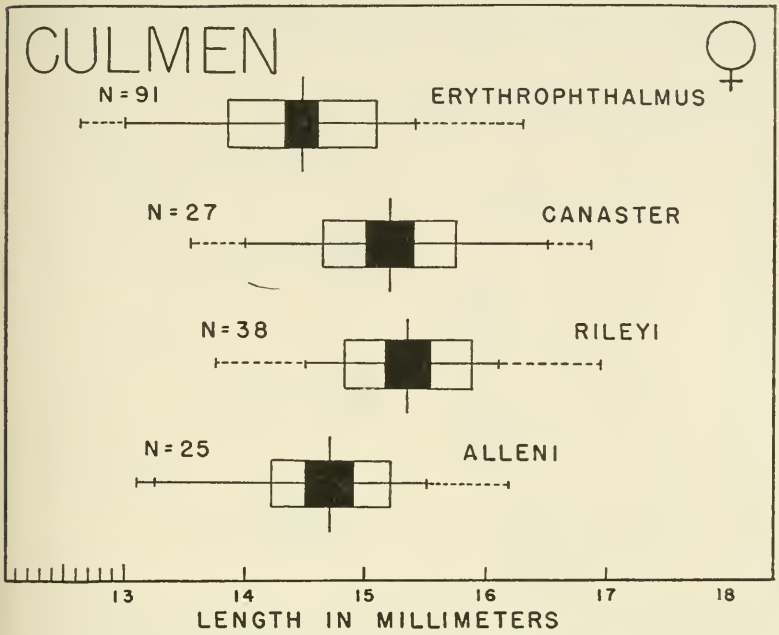

Figure 8. Variation in culmen length of females. See page 304 for explanation of figure.

erythrophthalmus, which averages 14.47 ± .07 mm. Correct identification of *erythrophthalmus* and *rileyi* obtains 78.0 per cent of the time. *Alleni*, averaging 14.71 ± .10 mm., is significantly smaller than *erythrophthalmus*, *canaster* and *rileyi*. The degree of separation of *alleni* from the other three races is less, however, than 75.0 per cent. The pattern of geographic variation in the females is the same as in the males.

Width of Lower Mandible

Males (Figure 9). Lower mandible width shows much the same geographic variation as does culmen length. *Canaster* has the widest bill, with a mean of 8.94 ± .03 mm. It is significantly different from *erythrophthalmus* in this measurement, the average width in the latter being 8.68 ± .02 mm. Within the northern race the western birds appear to have a slightly larger bill, with a mean of 8.72 ± .03 mm. This is near the borderline of significance in relation to the eastern birds, with a mean of 8.61 ± .02 mm. The material examined from the northcentral area has a mean mandible width of 8.61 ± .03 mm.

It shows no significant difference from the adjacent segments to the east and west.

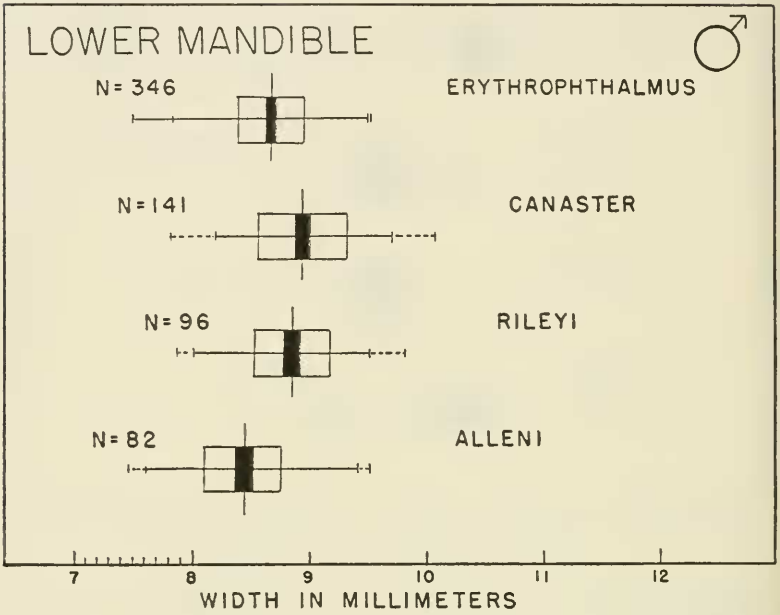

Figure 9. Variation in width of lower mandible of males. See page 304 for explanation of figure.

The bill of *rileyi* has a mean width of 8.85 ± .03 mm., which is not significantly different from that of *canaster*. It is, however, significantly different from *erythrophthalmus*. *Rileyi* is separated from *alleni* 74.3 per cent of the time.

Alleni has a smaller bill, averaging 8.48 ± .04 mm. A significant difference is shown in relation to *canaster* and *rileyi*. *Alleni* is separable from *canaster* 74.5 per cent of the time.

Of interest is the fact that *erythrophthalmus* and *alleni* show no difference in this character. Once again a northwest-southeast gradient is present, with maximum size in *canaster* and *rileyi*.

Females (Figure 10). The width of the lower mandible is of no diagnostic value in this sex. *Canaster* and *rileyi* have the greatest average width, 8.69 ± .05 and 8.79 ± .07 mm., respectively. They are not significantly different in this character. *Erythrophthalmus* averages slightly smaller (8.60 ± .04 mm) but is not significantly different from *canaster* and *rileyi*. *Alleni* is significantly smaller than

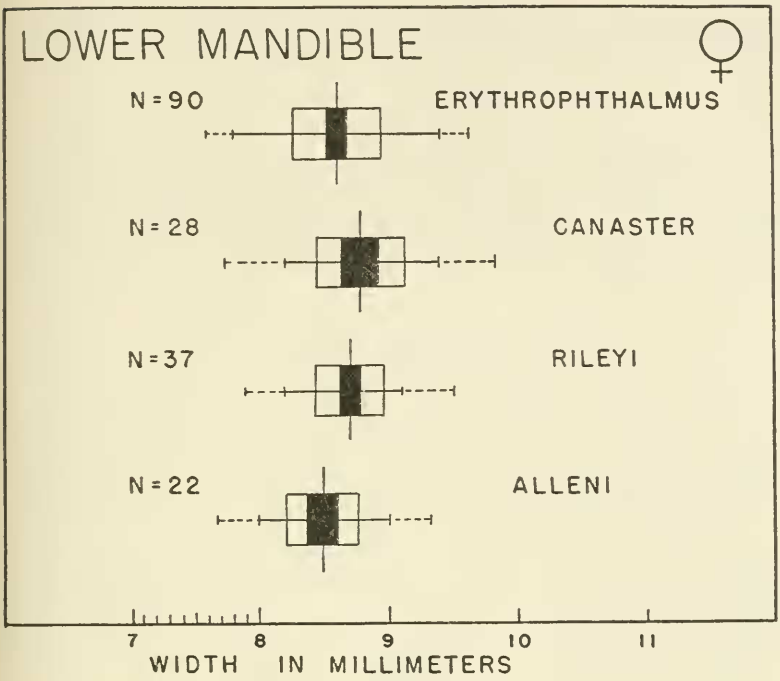

Figure 10. Variation in width of lower mandible of females. See page 304 for explanation of figure.

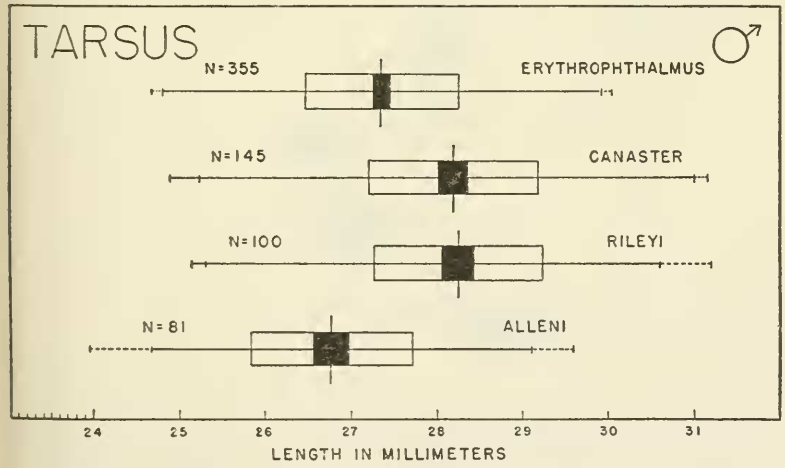

Figure 11. Variation in length of tarsus of males. See page 304 for explanation of figure.

rileyi and *canaster*, averaging 8.47 ± .06 mm. *Alleni* and *erythrophthalmus* are not significantly different from each other.

Tarsus Length

Males (Figure 11). The length of tarsus shows much the same geographic trend of variation as do the characters previously discussed. *Rileyi* and *canaster* have the longest tarsi, 28.25 ± .10 and 28.19 ± .08 mm., respectively. The difference is not statistically significant in this case.

Erythrophthalmus has a shorter tarsus, averaging 27.37 ± .05 mm. Although the tarsus is significantly different from that of *canaster*, *rileyi* and *alleni*, the character is of no diagnostic value.

Alleni has the shortest tarsus, average length being 26.78 ± .11 mm. Tarsus length is of diagnostic value in separating *alleni* from *canaster* and *rileyi*. In *canaster-alleni* separation, 76.8 per cent correctness of identification is achieved, and in *rileyi-alleni* 77.3 per cent.

Within the population here considered as *erythrophthalmus* I find no significant difference in the three samples studied. The eastern sample averages 27.42 ± .06, the central sample 27.05 ± .01, and the western sample 27.50 ± .09 mm. Ridgway obtained the same results in his earlier study, the nine eastern and eight western males each averaging 28.45 mm.

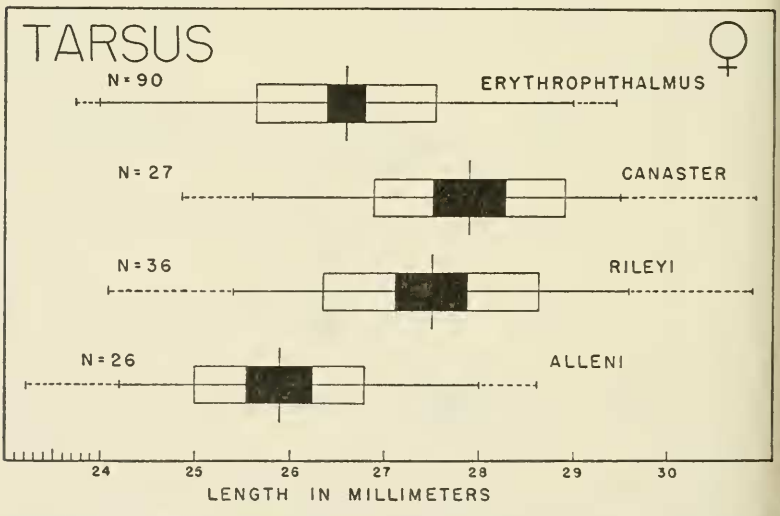

Figure 12. Variation in length of tarsus of females. See page 304 for explanation of figure.

Females (Figure 12). *Alleni* has the shortest tarsus, averaging 25.89 ± .18 mm. It is significantly different from *erythrophthalmus,* which averages 26.60 ± .10 mm. *Alleni* is 80.0 per cent separable from *rileyi,* whose tarsus averages 27.54 ± .19 mm. There is 85.5 per cent separation of *alleni* from *canaster,* whose tarsus averages 27.91 ± .20. *Canaster* and *rileyi* are not significantly different from each other in this character. *Erythrophthalmus* and *canaster* are 75.5 per cent separable. Less than 50 per cent separation obtains in *rileyi-erythrophthalmus* samples. The pattern of geographic variation is the same as that found in the males.

Middle Toe Without Claw

Males (Figure 13). *Canaster,* with a mean middle toe length of 20.19 ± .07 mm., has the longest toe, and is significantly different from *erythrophthalmus, rileyi* and *alleni* in this measurement. Nevertheless, only in the case of *alleni* and *canaster* is this character of diagnostic value, furnishing 78.3 per cent correct identification.

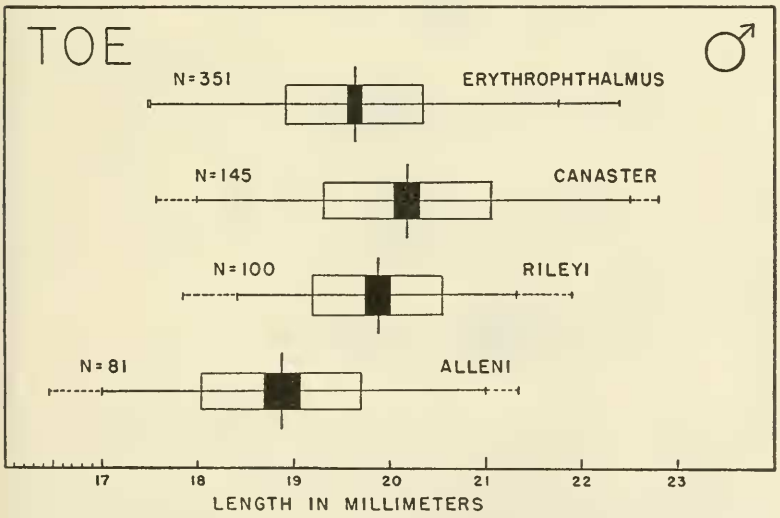

Figure 13. Variation in length of middle toe without claw of males. See page 304 for explanation of figure.

Rileyi has the next smallest middle toe, averaging 19.89 ± .07 mm. As pointed out above, it is significantly different from *canaster* in this measurement. In addition it is significantly different from *alleni* to the south and from *erythrophthalmus* to the north.

The toe of *erythrophthalmus* averages 19.64 ± .04 mm. This is significantly shorter than that found in *canaster* and *rileyi*, and significantly longer than that found in *alleni*. No significant difference was found in the samples examined from the eastern, central and western portions of the range of *erythrophthalmus*. Ridgway found that there was little difference in his nine eastern and eight western males. The average middle toe measurement was 19.81 and 19.56 mm., respectively.

Alleni has a much shorter toe than any of the other races, averaging 18.88 ± .09 mm. On the basis of this measurement *alleni* is separable from *canaster* in 78.3 per cent of the material examined. It is also separable in 75.0 per cent of the cases from *rileyi*. Correct separation from *erythrophthalmus* is possible in less than 70 per cent of a mixed sample of the two populations.

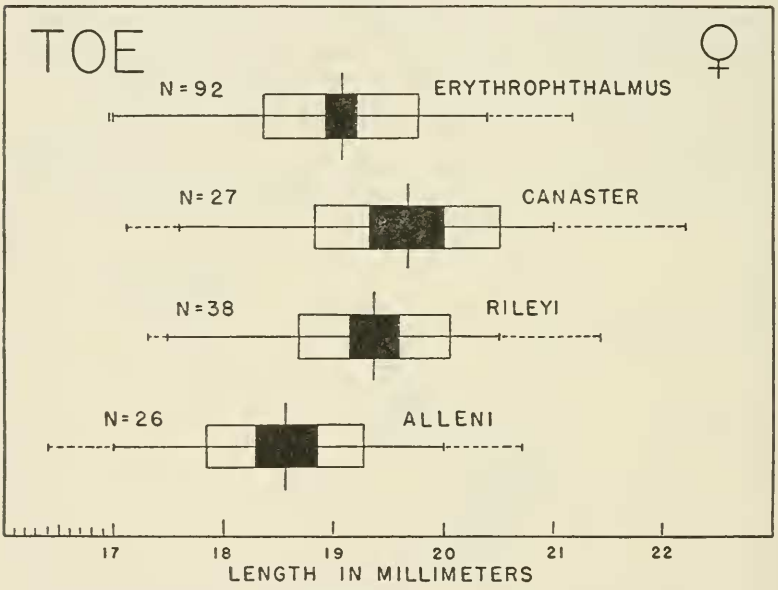

Figure 14. Variation in length of middle toe without claw of females. See page 304 for explanation of figure.

A general northwest-southeast clinal trend is observable in this character as in the others already discussed — maximum size occurring once again in *canaster* and *rileyi*, with diminishing size to the northwest and southeast.

Females (Figure 14). The middle toe in the female is not as variable

as in the male, although the same pattern of geographic variation appears. *Canaster* and *rileyi*, not differing significantly from each other, have the longest middle toes, averaging 19.66 ± .16 and 19.38 ± .11 mm., respectively. *Canaster* is significantly different from *erythrophthalmus*, which averages 19.06 ± .08 mm., and from *alleni*, which averages 18.57 ± .14 mm. Accuracy of 76.3 per cent is attained in separation of *canaster* from *alleni*. *Rileyi* is significantly different from *alleni*, but not from *erythrophthalmus* in this measurement.

Tail Spot: Tail

Males (Figure 15, upper). The ratio of extent of white on the outermost rectrix to length of tail proves to be of value in separating *erythrophthalmus* and *canaster*. In these two races the tail length and tail spot vary reciprocally, and for this reason the differences are magnified by calculation of this simple ratio. In *erythrophthalmus*, the tail spot is 39.36 ± .27 per cent of the tail length, and in *canaster* the percentage is 32.59 ± .45. This furnishes 74.5 per cent separation of these two forms.

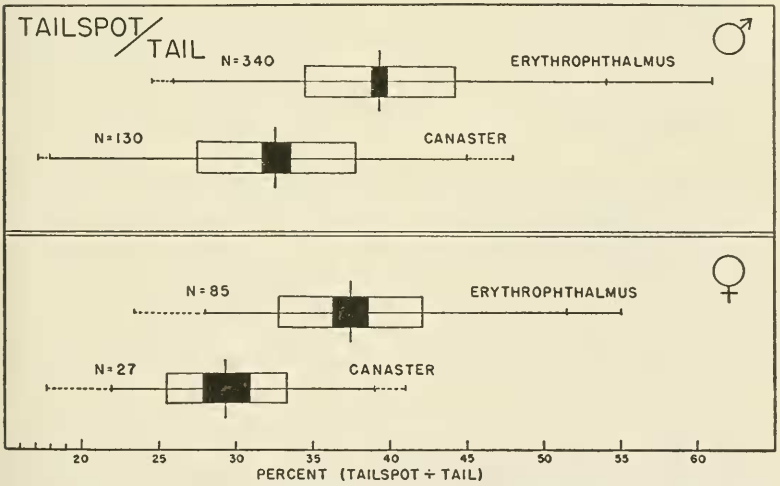

Figure 15. Variation in length of white spot on outermost rectrix: males (upper) and females (lower). See page 304 for explanation of figure.

Females (Figure 15, lower). In the females *P. e. canaster* has a mean of 29.41 ± .74 per cent, and *erythrophthalmus* a mean of 37.47 ± .51 per cent. The disproportionate increase in length of tail spot to length

of tail makes for an even greater divergence in this sex, with 82.3 per cent separation obtaining.

Number of Rectrices Showing White on the Inner Web

Males and Females (Table 20). The greater extent of white on the inner web of the outermost rectrix in the northern races has been commented on earlier. In addition to extent of white it is also true that more individual rectrices show white in the northern population. The

Table 20
Variation of White on Rectrices
Number of pairs involved, expressed in per cent of total sample

	Subspecies	*Pairs of Rectrices with White*				
		1	*2*	*3*	*4*	*5*
MALES	*erythrophthalmus* (N = 347)		0.6	43.8	52.7	2.9
	canaster (N = 143)		2.1	75.5	22.4	
	rileyi (N = 97)		7.6	87.0	5.4	
	alleni (N = 79)		32.9	59.5	7.6	
FEMALES	*erythrophthalmus* (N = 89)		1.1	69.7	29.2	
	canaster (N = 25)		12.0	80.0	8.0	
	rileyi (N = 24)		20.0	79.2		
	alleni (N = 24)	4.2	75.0	20.8		

males in *P. e. erythrophthalmus* furnish the upper extreme, occasionally showing white on as many as five pairs of feathers. One female of *alleni* showed white on only a single pair. In general males tend to show white on more feathers than do females. The character is of little diagnostic value in relation to the populations but may prove helpful in individual identifications. Table 20 presents the data for this character.

Iris Color

Males and Females. Variation in iris color presents some difficulty in analysis for the reasons outlined in the introduction of the present paper. *P. e. erythrophthalmus* and *P. e. alleni* may be largely disregarded, since they uniformly have "red" and "white" irides, respectively. *Canaster* and *rileyi*, on the other hand, show mixtures in varying degrees of these two basic colors, and it appears that a knowledge of variation in iris color is quite important in gaining a clearer understanding of the racial relationships within the species.

Basically it is readily apparent that the intermediate eye colors are found in the areas of geographic intermediacy between the northern and southern races (Map 3). The map does not attempt to weigh the different iris colors according to relative percentages but simply furnishes a record of the limits of distribution of the three colors plotted. Arbitrary classification of the multiplicity of color notations made by various collectors was quite necessary. An attempt was made to be as conservative as possible in the interpretation of the color notation made on the labels. Weighing of the several colors was accomplished by use of the Chi-square test (Table 21). The degree of association of iris color with geographic locality is very high, so high that it may safely be assumed that the probability of such distribution occurring by chance alone is nil.

Iris color in *canaster* may be "orange" or "yellow" but it is usually red (84.25 per cent). In *rileyi* the color may be "red" or "orange" but it is usually yellow (79 per cent).

Material from the type localities is unfortunately slightly confusing. A *canaster* topotype (JCD 269) taken near Mobile, Alabama, had yellowish irides. Specimens (PB 15771 and JCD 263) taken by Dr. Pierce Brodkorb and myself near Brunswick, Georgia, were close to salmon (10-G-3) and buff (10-I-5), respectively.

There seems to be no reason to call upon any genetic principle more complicated than multiple factors or multiple alleles for explanation of this distribution. No clues are available at present to indicate the number of genes involved, but the almost perfect blending of pigments seems to follow the pattern usually associated with these types of inheritance. The splotchy distribution of color found in some individuals, and reports of pie-shaped segments of different colors in the irides furnish further support for this hypothesis.

The iris color in juvenals has apparently been overlooked by most investigators dealing with the pale-eyed birds of the southeast. Maynard (1881: 114) states that Florida nestlings have light brown irides. The young birds of the north have iris color that is usually described as "muddy brown", "brownish", "sepia-brown", "dark

Table 21

Variation in Iris Color

The Alabama, Mississippi, Louisiana, west Florida and central Georgia records represent *P. e. canaster*.

The coastal North Carolina, coastal South Carolina and southeastern Georgia records represent *P. e. rileyi*.

IRIS COLOR

LOCALITY	MALES	RED	ORANGE	YELLOW
	Ala., Miss., La., west Fla., central Georgia	119	19	4
	Coastal N. C., S. C., southeast Georgia	2	12	59

$\chi^2 = 158.54$ (Surely significant)

IRIS COLOR

LOCALITY	MALES	RED	ORANGE	YELLOW
	Ala., Miss., La., west Fla., central Georgia	20	3	0
	Coastal N. C., S. C., southeast Georgia	0	7	20

$\chi^2 = 41.52$ (Surely significant)

IRIS COLOR

LOCALITY	BOTH SEXES	RED	ORANGE	YELLOW
	Ala., Miss., La., west Fla., central Georgia	139	22	4
	Coastal N. C., S. C., southeast Georgia	2	19	79

$\chi^2 = 190.67$ (Surely significant)

brown", "brown", or some other color designation which appears to fall in the brown category. Sutton (1935: pl. III) pictures a 15-day old male bird from Michigan as having dark brown irides. Fully-fledged juvenals (JCD 180) taken in Florida, and in Georgia, 5 miles north of Brunswick, Glynn County, (JCD 260 and 264) have the iris color near "Pale Neutral Gray" in Ridgway's system and 15-A-3 in Maerz and Paul.

Plumage Characteristics of Females

Efforts to establish color classes for the various parts of the plumage were not successful. The range and variability of the colors is such that clear-cut differences are not observed. Four areas of plumage were scrutinized: back, flanks, breast and crown. After it was decided that it was not possible to use the techniques of color classes for statistical analyses of the plumage characters, the material was identified on the basis of mensural characters and notations made as to range of color in the various races.

The possibility of color change due to age of skins was considered, and old skins (1930 and earlier) were compared with fresh material (1940 and later). I was not able to detect any change due to museum age.

Back color. *P. e. erythrophthalmus* as a whole is more reddish brown than *P. e. alleni* and *P. e. rileyi*. Some skins (CM 2290) are quite reddish (15-A-12); others (USNM 363240) though reddish are very pale, (15-H-9). USNM 23598 is much darker (15-H-9) than the average. USNM 56535 is dark but not quite as reddish (8-H-12). The average color of this race appears to be best represented by UMMZ 96950, (15-J-8). Birds in fresh plumage are slightly darker than those showing wear, and a skin from Jackson County, Michigan (GMS, Oct. 11, 1949), is typical of these fresh-plumaged birds (8-E-11).

In *P. e. rileyi* the older skins show more red pigment than the fresh material. In this case, however, the older material is from the northern and inland localities where *rileyi* meets *canaster* and *erythrophthalmus*, both of which are on the average more reddish than *rileyi*. MCZ 208060 is typical (15-C-11). In this case it seems quite likely that the difference is due to geographic rather than temporal factors. The coastal localities provide material that is very similar to *alleni* in general color (15-E-7). Some individuals are much darker (JCD 258 and PB 15772).

The *canaster* sample shows no detectable differences due to age of skins. USNM 38247 (1946) matches CNHM 166708 (1916) in back color (15-E-11). The average color of the sample is typified by USNM

340494 (15-E-9). The material examined appears to be more olive and reddish than the *alleni* sample and slightly grayer than *erythrophthalmus*.

Alleni is conspicuously grayer than *erythrophthalmus* and *canaster* but not grayer than *rileyi*. Some individuals, AMNH 368079 (15-J-11), approach *canaster* in redness, but the general color of the sample is typified by USNM 261709 (15-E-7). There is no detectable change in color due to age of skin.

The color of the back does not show any sharp breaks which are correlated with geographic distribution. The northern race shows much more red pigment than the peninsular Florida population, but in the intervening populations the colors are apparently the result of varying admixtures of these extremes.

Flanks. P. e. erythrophthalmus has darker flanks on the average than have the other races. Average color is represented by USNM 339625, 257922 and CM 2762 (13-H-12). Some skins are much darker (14-E-12) than the average, as in USNM 268666, 235598, 306445 and UMMZ 66998. The lightest flanks (13-J-10) in the sample at hand are from a skin taken at Wheeling, West Virginia, on May 2, 1936, now in the M. M. Peet collection.

P. e. rileyi has very uniform coloration of the flanks and is quite like *erythrophthalmus* in color. The darkest specimen (MCZ 10355) is 14-I-11, the lightest (USNM 298673) is 13-K-11, and the average color, as represented by USNM 382391, is 14-C-12.

P. e. canaster is more variable in flank color. The darkest specimen, USNM 382361, is 14-E-12, and the lightest is 13-K-9. The average color is lighter than *erythrophthalmus* and slightly darker than *rileyi*. It is represented by 13-K-9, as found in USNM 378909.

P. e. alleni has much lighter flanks than the other races. USNM 261711, with 13-D-11 flanks, is considered as being typical. The darkest color present in my material is 13-G-10 (USNM 133091). The lightest, 12-I-10, is found in LSU 8148.

Breast. P. e. erythrophthalmus is quite variable in the coloration of this area of plumage. Skins from the far northwest, Grafton, North Dakota, are very dark, 15-C-12, as seen in UMMZ 66998 and 56535. The lightest breast in this sample, 14-H-9, is found in USNM 348791. Some are quite reddish, 15-A-12, USNM 306445. The average color appears to be 14-K-9, as found in AMNH 367858.

P. e. rileyi has more gray pigment (or less red) than *erythrophthalmus*. The grayest, 15-A-6, is JCD 259, while the most reddish, 15-C-11, is found in MCZ 208060. The average color is best represented in MCZ 212455, as 15-C-9.

P. e. alleni shows considerable variation in breast color. The average, 14-J-9, found in USNM 300219, is paler and less red than *rileyi* and *canaster*. JCD 176 is as reddish as the average *canaster* color, 15-C-12. USNM 261711 is the darkest in this sample, 15-C-6, and LSU 8148 is the lightest.

Crown. *P. e. erythrophthalmus* has the darkest crown of the four races. USNM 338022 and UMMZ 56535 are very dark, 8-E-12. UMMZ 74532 is the lightest, 14-E-8. Some skins show considerable redness, as in CM 2290, which is 15-A-12. GMS 8917 appears to be representative of the average color, 8-L-12.

Canaster is paler than *erythrophthalmus*; the average color, found in USNM 258980, is 7-A-12. One skin, USNM 379723, is very dark, 8-H-12. The lightest color observed, 15-C-12, occurs in a specimen taken in Fulton Co., Georgia, May 2, 1928 (M. M. Peet collection).

P. e. rileyi is slightly paler on the top of the head than is *canaster*. An average skin is represented by USNM 298673, 8-H-11. MCZ 208060 (see breast) is the most reddish, 7-A-12. PB 15772 is the darkest, 8-J-12. AMNH 55406 is very light, 14-L-10.

Alleni is the palest of the four races. The average color, 15-E-12, is present in USNM 261708. JCD 176 (see breast) is quite reddish, 14-C-12. The darkest specimen, AMNH 368317, is 8-H-12.

Summary. There appears to be a general intensification of red and black pigments in the northern areas in all the feathers showing color. There is considerable difference between *erythrophthalmus* and *alleni*, but in so far as I am able to determine, the blending of colors is so gradual and variability is so excessive that coloration is of taxonomic value in this species only when large series are available for comparison.

Plumage Characteristics of Males

Back, Crown and *Breast*. The color of these areas of plumage varies little in the four races. The average color of the back in *erythrophthalmus* is Sooty Black[1]. *Canaster* averages slightly paler, Olivaceous Black (3). Olivaceous Black appears to represent the average color in *rileyi*. *Alleni* is conspicuously paler, Iron Gray. In all of the races there is considerable individual variation, and Sooty Black individuals occur in all four. As a result of wear and bleaching, the darker races occasionally show very pale back colors. The color of the crown and breast presents the same pattern of geographic variation as does the back. To my eye the color of these areas is the same as that of the back.

[1] Colors approaching black are not adequately treated in Maerz and Paul, and Ridgway (1912) was used for these colors.

Flanks. *P. e. erythrophthalmus* has the richest color in the flank feathers. The darkest specimen examined was CM 2831, which was 6-A-12. CM 7576 was the lightest of the northern birds, 12-D-11. The average color was matched by 5-D-12 in AMNH 367998.

Canaster is slightly paler than *erythrophthalmus*, darker than *alleni*, and paler than *rileyi*. The darkest specimen, USNM 378920, was 13-K-11. The average color present in this race is 13-D-11, as found in USNM 338901. Some birds are quite light, as light as average *alleni* specimens. The lightest, 12-F-10, was found in USNM 240167.

Rileyi shows little variation in flank color. In a series of eight birds from the type locality seven are remarkably uniform. One (JCD 256) is as dark as the darkest specimen of *P. e. erythrophthalmus*, 6-A-12. The average color is near 13-C-12, as in JCD 253. The palest specimen, JCD 255, is 12-H-8.

The palest of the races, *alleni*, has an average flank color which is near 12-F-10, as present in JCD 178. In the only cotype of this race available to me, MCZ 10721, the color is 12-G-10. JCD 249 is the palest specimen examined and is near 11-H-8. The darkest flanks were found in JCD 178, 13-A-12.

Summary. In this sex the same general intensification of color occurs in the northern races. *Alleni* is conspicuously paler in all plumage showing color. *Rileyi* and *canaster* are intermediate in color. The sample representing *canaster* shows much greater variation than does that of *rileyi*.

NON-GEOGRAPHIC VARIATION

The most unusual individual variant was discovered in a bird of the year taken by W. H. Osgood. The bird was collected in Maryland, 10 miles north of Washington, D. C., on August 1, 1897, and is now No. 367895 in the collection of the American Museum of Natural History. The specimen is labeled as a male, and the greater part of its plumage is clearly of this sex. A large patch of female plumage, however, is present on the upper back, extending forward to the neck and around the right side. No flight feathers appear to be involved. Heterosexual plumage changes have been recorded on many occasions in domestic birds, and Brodkorb (1935) reports what may have been a similar situation in *Falco sparverius*. His explanation of that case as gynandromorphism does not furnish an adequate solution for the pattern present in this case. I am inclined to believe that a non-bilateral pattern is the result of somatic change rather than hormone interplay. In this case there is no information available concerning the gonads, but it does not seem likely that such a spotted distribution

would be produced in a sexually dimorphic character by lack of balance in the male and female hormones.

If it is assumed that the towhee has the same type of sex determination as poultry, then another proposal can be made. If this specimen developed from a fertilized ovum carrying a pair of X chromosomes, as such it was destined under normal circumstances to become a male. Distortion of the normal mitotic processes on many occasions has been known to result in the deletion of parts of or whole chromosomes. The number of daughter cells showing the effects of the deletion is dependent upon the stage of development of the individual at the time the aberration occurs. Development of female secondary sex characters from the heteroploid cells, produced in such fashion, is due to the absence of the X chromosome rather than the presence of the Y. Such a chain of events appears to have occurred in this individual.

White-tipped feathers at the bend of the wing, involving the tips of the secondary coverts, and varying degrees of white streaking in the scapulars have long caused speculation as to the affinities of *P. erythrophthalmus* and *P. maculatus* (Baird, Brewer and Ridgway 1874, Allen 1878, Coues 1878, and more recently by Sibley 1950.) The appearance of white at the above mentioned points has been looked upon as evidence of an exchange of germ plasm between the eastern and western species, or as an indicator of common origin of the two forms.

There seems to be some evidence that such an exchange does at least have the opportunity to occur in that the ranges of the two forms closely approach each other. In the breeding material examined in the course of the present study varying degrees of white tipping of the secondary coverts was found in 136 male and 29 female specimens, taken over the entire range of the eastern forms, even in Florida and New York. USNM 302208, a male taken near Athens, Georgia, on February 24, 1930, shows this spotting and streaking of the coverts and scapulars to a marked degree. The iris color, as recorded by T. D. Burleigh, was "dirty yellow." This would seem to rule out the possibility that the bird was a stray from the west.

On the basis of mensural characters the Georgia bird is identified as *P. e. canaster*. The degree of marking is equal to that found in GMS 10172, a male taken at Lincoln, Nebraska, on May 13, 1946. George M. Sutton, the collector, comments on the label "white on back reduced — *P. m. arcticus* approaching *P. e. erythrophthalmus*."

The recommendation made by Sibley (*op. cit.*) that *erythrophthalmus* and *maculatus* be considered conspecific would seem to be a wise action. Although I did not have sufficient material at hand to critically analyze the geographic distribution of this variation I am inclined to think

that it is indicative of common origin rather than interbreeding in recent time.

Albinism is quite rare in the species. Only one specimen, an adult female *P. e. erythrophthalmus* from North Carolina, AMNH 104434, shows any appreciable degree of this plumage change. The iris color was recorded as "pearl gray." The pattern of white is bilaterally symmetrical and extends from the front to the rectrices. The neck is white, and the contour feathers of the body are generously sprinkled with white. Several of the primaries and secondaries are involved. Twenty-one other specimens were found showing from one to perhaps several hundred randomly placed white feathers.

In both sexes there is a variation which involves the tips of the crown feathers. In seven specimens from scattered localities these feathers were conspicuously tipped with rufous. This variation may be still another indication of the affinity that exists between the eastern and western segments of the populations. The pattern presented by this variant is similar to that found by Sibley in the hybrid population of Cerro Viejo, Jalisco. (See his plate 12, MVZ numbers 115243 and 115215).

MIGRATORY BEHAVIOR

It has long been known that *P. e. erythrophthalmus* moves well southward during the winter. The practicality of distinguishing red-eyed from pale-eyed individuals in the field has had two effects: (1) to confuse the literature with numerous sight records of this race when the birds may have been *P. e. canaster* and (2) to allow the retention of Howell's original concept of the sedentary nature of *canaster*. It is felt that on the basis of the present study, valid criteria for the identification of the four races have been determined. On the basis of these criteria, wintering material has been examined and identified with interesting results. Admittedly some of the individual identifications are not correct. However, it is assumed that sufficient numbers of specimens were at hand to minimize the danger of false conclusions with reference to the general winter behavior of the four races.

Map 4 shows the result, in summary form, of this phase of the investigation.

P. e. erythrophthalmus withdraws practically all of its numbers from the breeding grounds. Some few individuals for unknown reasons do remain in the northern United States during the winter, but the majority leave, spreading south and west as far as Nueces and Lee Counties, Texas, and south and east in Florida as far as Hillsborough, Okeechobee and Volusia Counties.

P. e. canaster, regarded by Howell as remaining on the breeding grounds during the winter, certainly does this, in so far as a portion of the population is concerned. On the other hand, winter specimens, taken in Florida as far south as Wakulla County on the northern Gulf Coast, indicate some post-breeding movement of individuals. In the material examined there were no specimens of *canaster* from the east coast of Florida. There are numerous winter-taken individuals of *canaster* from south-central Georgia, in the area occupied by *rileyi* during the breeding season. There appears to be a slight retreating of the population along the northern extent of its breeding range. Winter specimens, with one exception, from southern Tennessee, northern Alabama, Mississippi and Louisiana are typical of *erythrophthalmus*.

P. e. rileyi spreads north, south and west, during the winter. The wandering to the north and west is not marked, but to the south *rileyi* extends its population to mid-peninsular Florida. Winter specimens of this race are available from as far south as Charlotte County on the west coast and Brevard County on the east coast. It is apparent, however, that many of the birds do remain within the breeding range outlined for this form. It is interesting to note that the series of cotypes established by Coues' action in describing the Florida race contains some four individuals (C. J. Maynard 2559, 2669, 2592, 2513) whose wing measurements as given indicate that they may have been wintering birds from the north (*rileyi*). This series was taken during February and March. Only one specimen of this series (MCZ 10721) was available to me, and it is typical of *alleni*. My measurement of 77.0 mm. for length of wing as compared with 2.92 inches [74.2 mm.] as given by Allen (1871) probably indicates that these earlier wing length figures represent "chord" measures.[1]

P. e. alleni apparently is largely sedentary. Howell (1932: 448) did not have records available for breeding birds in the extreme southern part of peninsular Florida but did indicate that *alleni* spread southward during the winter to this area. Summer specimens (JCD 185, UMMZ 114394 from southern Dade County, Florida) furnish evidence that this form now extends into the extreme southern tip of Florida as a breeding bird as well as in winter. JCD 185 was taken while in company with females and juvenals. There is no evidence of any extensive post-breeding northward wandering in this race.

[1] Two discrepancies in the table of measurements given by Allen are worthy of note. A wing length of 3.90 inches (99.1 mm.) for MCZ 10726 must be due to error in measuring or in publication. This length far exceeds any seen by me in any of the four races. There is duplication of MCZ 10729 in having this number assigned to two of Maynard's skins, 2665 and 2669.

VARIATION IN RELATION TO ENVIRONMENT

Ecological Rules

The data available have been examined from the standpoint of several pertinent ecological rules suggested as being applicable to warm-blooded vertebrates. Mayr (1942: 88–92) has summarized these rules and his wording of them is followed below.

Bergmann's Rule. "The smaller-sized races of a species are found in the warmer parts of the range, the larger-sized races in the cooler districts." Insufficient data concerning body weight were available, and hence this measure of size could not be examined adequately. Other measures, wing, tail, culmen, width of lower mandible, tarsus and middle toe, which may possibly be indicators of total body size[1], present a puzzling picture. *Alleni* is smaller than any of the other races in respect to these characters. In keeping with Bergmann's Rule the adjacent races to the north, *canaster* and *rileyi*, are larger. *Erythrophthalmus* from still further north however, is smaller than the intermediate races, though not as small as *alleni*. It is of course difficult to estimate the selective effect of lowered winter temperatures on migratory forms. *Erythrophthalmus* moves well down into those areas where a large portion of *canaster* remains as a resident form during the winter, and for the most part does not experience lower temperatures than the resident southern individuals. A segment of the population of *rileyi* accomplishes this same movement in relation to *alleni* and as a population is probably not subjected to much lower temperature than the peninsular Florida race.

In this case, then, it appears that if the breeding ranges are considered, *alleni* follows the rule in relation to *canaster*, *rileyi* and *erythrophthalmus*. *Canaster* and *rileyi*, however, do not seem to follow the rule in relation to *erythrophthalmus*.

Allen's Rule. "Protruding body parts, such as tails, ears, bills, extremities, and so forth, are relatively shorter in the cooler parts of the range of the species than in the warmer parts." Lack of information concerning total body size made valuation of this rule difficult. Examination of culmen length, mandible width, tarsus and toe, however, shows that the most southern race is the smallest of the four. *Canaster* and *rileyi* are larger than *alleni* in these measurements but *erythrophthalmus* is smaller than the former two. In this case *erythrophthalmus* may conform to the rule in relation to *canaster* and *rileyi*. *Alleni*, however, apparently does not conform in relation to any of the other forms.

[1] Miller (1941: 354), in his detailed investigation of variation in *Junco*, concluded that wing and tail length in this genus were largely independent of body size.

Gloger's Rule. "The melanins increase in the warm and humid parts of the range. Reddish or yellowish brown phaeomelanins prevail in arid climates where the blackish eumelanins are reduced. The phaeomelanins are reduced in cold climate, and in extreme cases also the eumelanin (polar white)." In examination of this rule it was felt that the breeding season was the critical period. For this reason July values for this environmental factor were examined (Weather Bureau: 1897). The breeding range of *alleni* has the highest relative humidity. The average for two stations is 83.0. *Rileyi* inhabits the next most humid area, two stations averaging 81.0. The range of *canaster* is slightly less humid, averaging 80.3 for six stations. The more northern and inland range of *erythrophthalmus* is considerably less humid; 12 stations average 70.2. In both the males and females the northern form, inhabiting an area of lowest relative humidity, shows an increase in the reddish pigments present. *Canaster* is grayer than *erythrophthalmus*. *Rileyi* shows more red on the plumage than does *canaster*, but not as much as *erythrophthalmus*. The plumage of *alleni* is not darker than these, but rather more gray, as if due to bleaching. Thus, *rileyi* and *alleni* appear to conform to this rule as a unit. *Canaster* and *erythrophthalmus*, when viewed together, also appear to conform to Gloger's rule. When the whole species is considered, however, a lack of conformity is evident.

Rensch's Clutch Rule. "The races of a species which live in the cooler parts of the range of that species lay more eggs per clutch than the races in the warmer parts of the range." Todd (1940) and Roberts (1932) report for western Pennsylvania and Minnesota, respectively, average egg clutches of four to five. Howell (1932) records the average size of clutch in Florida as three. Sprunt and Chamberlin (1949) indicate clutches of two to five for *canaster* in South Carolina. With the scanty data available general agreement with this rule appears to be the case.

Rensch's Wing Rule. "The wings of races that live in a cold climate or in the high mountains are relatively longer than those of the races that live in the lowlands or in a warm climate." *Alleni* is the only race which shows conformity with this rule. In its relationship to *rileyi*, *canaster* and *erythrophthalmus*, the wing of *alleni* shows considerable shortening. *Erythrophthalmus*, however, has a mean wing length which is not longer than that found in *canaster* and *rileyi*, but shorter.

Mayr's Rule (1942: 92). "Races in the cooler climates are more strongly migratory than the more southerly one." *Pipilo erythrophthalmus* does not conform to this rule as indicated in the discussion of migratory behavior in this report.

Biotic Areas

Dice's (1943) Biotic Provinces have been scrutinized in this connection and little conformity of racial distribution with those provinces is evident except in *erythrophthalmus*. This race is distributed in an approximation of Dice's Canadian, Illinoian and Carolinian provinces. The other three races, however, are mainly contained in his single Austroriparian province.

Conformity of racial distribution of towhees to the Life Zones of Merriam et al. (1910) presents much the same picture. *P. e. erythrophthalmus* breeds in the eastern part of the Upper Austral and Transition zones. The differentiation of *canaster*, *rileyi* and *alleni* within the Lower Austral Zones does not conform with the proposals of either Dice or Merriam with regard to environmental sameness for this area.

Temperature Zones

Visher (1944) presented a series of seventeen maps concerned with freezing temperatures in the United States. His Figure 17, based on the duration and severity of freezing temperatures, divides the United States into six zones. These zones approximate fairly closely those of Merriam, except in the extreme southeast. Visher's data indicate that southern Florida, northern Florida and the Gulf Coast, and the Piedmont and Coastal Plains areas of the southeast should be considered as different from one another in respect to freezing temperatures. Calhoun (1947) concluded that there was correlation of size in *Passer domesticus* with the thermal lines drawn by Visher. Visher's zones 4, 5, and 6 cover the range of *erythrophthalmus*. The southern limit of zone 4 closely approximates the southern limit of this race during the breeding season. Zone 3 contains *canaster* in its western, and *rileyi* in its eastern portion. The southern limit of this zone conforms favorably with the southern limit of these two races. *P. e. alleni* ranges over Visher's zones 1 and 2. There is approximate conformity of racial distribution to these zones.

It appears that the various ecological rule, biotic province, life zone and temperature zone correlations are of most importance in dealing with non-migratory species. Migrating populations for the most part avoid the selective effect of lowered winter temperatures by simply moving away from them. The few stragglers that remain in the far north must be of little importance when considered with respect to the whole population.

Historical Factors

In view of the fact that present environmental factors do not appear to furnish an entirely adequate explanation for the geographic variation within the species, some other factors must be considered. As mentioned earlier great difficulty is experienced in arriving at a conclusion as to whether the (1) southeastern races represent an extension of the range of the northern population (or vice versa) or whether (2) *canaster* and *rileyi* are representative of extensions of formerly isolated populations which are now meeting and intergrading in the middle ground of the southeast.

The possibility of stabilization of genotype as a result of a narrowing front as the continental population pushed south into Florida must be considered. The narrowing would not become pronounced until the species moved down onto the Coastal Plain. It furnishes no explanation for the differentiation of *canaster* and *erythrophthalmus*, whose line of junction is not appreciably narrowed. The junctions between *canaster* and *rileyi*, and *rileyi* and *alleni* are successively narrower. It is possible to visualize, particularly in the case of *alleni*, stabilization taking place as a result of this radical narrowing. *P. e. alleni*, however, is not the most perplexing of the races here considered. In many respects, as already noted, this form shows the effects of environmental selection in agreement with several of the ecological rules surveyed.

In connection with the second proposal, a review of some of the geological events which occurred in the Cenozoic is to the point. Cooke (1945: 3) concludes that the Floridian Plateau has always been a part of the continental mass as distinguished from the deep sea. There appears to be little question that throughout Tertiary time peninsulas or islands of varying shapes and sizes existed in the present area which constitutes Florida. There certainly have been periods during pre-Oligocene epochs when all of this area was under water, but the evidence available seems to indicate the possibility that several island areas may have been above water ever since that time.

White (1942: 29–47, figs. 5–9) discusses the history of this area based on evidences from geology and paleogeography. Much of his information comes from a vertebrate fossil deposit in Gilchrist County, Florida, near Bell. He concludes that following the withdrawal of the Eocene seas, there was a series of crustal movements which resulted in the formation of the Central Florida Dome. At the same time there was a down-warping of the strata across the northern end of the plateau to form the Okefenokee Trough. During the Lower Oligocene the sea invaded the Okefenokee Trough only far enough to form a large bay at either end, with a pedunculate land mass extending southeastward from the mainland of North America.

During Middle Oligocene (Marianna time), with further crustal movements occurring, there was a deepening of the Okefenokee Trough, and the Gulf communicated with the Atlantic across north Florida and south Georgia through straits 50 or 60 miles wide. At the close of this period of submergence there was a general withdrawal of the seas, and Florida was again connected with the mainland.

The late Upper Oligocene saw the reduction of this land mass to a small island, located in what is now the northwestern part of the peninsula, roughly 150 miles from the nearest mainland. The vertebrate fossil material at Bell, Florida, contradicts Schuchert's (1935: 231) earlier concept of the general submergence of the Florida peninsula by the advancing Lower Miocene seas. White (*op. cit.*: 42) states:

> "During the period of time represented by the fluvial deposit in Gilchrist Co. [Lower Miocene], Florida was a limestone island cut off from the mainland by a shallow sea fifty or sixty miles wide. In Tampa time Florida was an elliptical island roughly 220 miles north-south by 100 east-west. . . .
>
> "If the structure of Florida. ..... during the Lower Miocene was at all similar to that of today the highest part of the island would have had an elevation of about 200 feet. This is not enough seriously to affect the climate. There is no reason to suppose that the climate was very different then than now."

Throughout the Miocene there was further withdrawal of the seas. It appears that from this time forward there has certainly been some land, in the form of large islands or a group of keys, present in central Florida.

The emerging land mass, indicated as having appeared during the late Miocene, in Pliocene time became a peninsula forecasting the shape of the state today. The area south of the present latitude of Lake Okeechobee was covered by a shallow sea (Campbell, 1940: 104).

During the Pleistocene, peninsular conditions were permanently established, following the several oscillations of sea level attendant to the fluctuation of the ice caps. The Pleistocene history of the extreme southeastern United States has been reviewed by Cooke (1939). He states that there were at least six fluctuations of sea level during this period — from 270 feet above, to 230 or 300 feet below the present level. The highest rise of water, attained at the beginning of the Pleistocene, produced the Brandywine Terrace. At this time all of Florida was submerged, except for a group or groups of islands located in what is now mid-peninsular Florida, at about the latitude of Tampa. A scattered chain of small islands extended northward into middle southeastern Georgia. Much of the present range of *P. c. rileyi* was

under water at this time. Following this high level of water, there was a fall to 230 or 300 feet below the present sea level; a rise of 100 feet above and an intermittent fall to 60 feet below; an intermittent rise to 25 feet above and a drop to an undetermined low; and a last rise to the present level. Cooke further states that there has been no crustal movement during this period, as evidenced by the unbroken beach terraces in this area created by the oscillations of sea level.

The present Florida race, *alleni*, may be a relict form. Carr (1940: 6) in his study of the relict herpetofauna of this area places the Florida relicts in two classes: "(1) those derived *in situ*, from living or extinct or subsequently modified ancestral stocks, either by isolation on a Pliocene island or islands (or as I believe less likely, on Pleistocene Islands), or else by ecesic isolation; and (2) those which represent the remnant of a once widespread pre-Pleistocene stock."

That birds inhabited these island and peninsular land masses there is no doubt. Wetmore (1943) has examined avian material from Pierce, Polk County, Florida, and from the Bell locality. The material from Bell has been assigned to Lower Miocene by White and contains "a peculiar shorebird of a hitherto unknown type, a dove, and a wood warbler." The shorebird has been designated by Wetmore as the type of an extinct family. The other two species have not been identified. The Pierce fossils have been attributed to Middle Pliocene deposits by White and consist of *Gavia palaeodytes* Wetmore, *Diomedea anglica* Lydekker and *Phalacrocorax auritus* (Lesson). These forms, all marine or aquatic in habits, do not necessarily indicate the existence of nearby land masses, except as the needs for breeding grounds arose. Of additional interest in connection with the present discussion of variation is Wetmore's comment concerning his assignment of the cormorant material of Pliocene age to the modern species. He says, "unquestionably they appear to belong to this the modern species. . . ."

Certainly the possibility exists that either during Pliocene or post-Pliocene time a segment of a continental population of birds might have become isolated in this area. The barrier causing isolation does not have to be visualized as consisting of simply the straits or narrow necks of land that have existed between Florida and the continent at various times during this period. Even with the connection re-established for varying periods of time, ecesic barriers may have prevented re-uniting of the previously isolated segments.

If these events have occurred then one might expect to find some evidence of their occurrence reflected in the present populations. In the review of the migratory behavior of the four races, it was pointed out that the movements of *rileyi* and *erythrophthalmus* are much more pronounced than those of *canaster* and *alleni*. If *rileyi* is viewed as the

northward extension of *alleni*, it may be thought of as returning to its point of origin during the winter. The same may be said of *erythrophthalmus* as it extended from the range of *canaster* northward, following the retreating glaciers of the Pleistocene. The blending of certain characters, such as iris color and tail spot are certainly not in disagreement with such a proposal. The intensification (enlargement) of others such as bill size, wing, tarsus and toe may be due to the hybrid nature of the intermediate populations.

In conformity with Allen's Rule, if *erythrophthalmus* is viewed as the extension of *canaster* northward, it is found that the extremities in this race do show reductions in size. There is no significant difference in wing size in these forms, in contradiction to Rensch's Wing Rule. Mayr's Rule on migration, however, confirms this view, as does Gloger's Rule on color. *Rileyi*, when compared with *alleni*, shows some increase in bill, tarsus and toe, in contradiction of Allen's Rule. The increase in wing length is in agreement with Rensch's Wing Rule, and the migratory behavior of these two races conforms to Mayr's Rule. In the same manner, as pointed out earlier, there is evidence of conformity with Gloger's Rule.

Habitat preference, particularly in the peninsular Florida race, is of interest. *P. e. alleni* shows definite association with the various scrub-type plant communities found near the coasts and in the central lake region. These plant communities are, according to Laessle (1942: 96), representative of the earliest stage of a xerosere, in the area he studied in Putnam County, Florida. Throughout the state they occur on old dune areas where the soil is almost pure white (St. Lucie) or yellow (Lakewood) sand. In this pioneer association, the only tree of any size is the sand pine (*P. clausa*), with a dense undergrowth of dwarfed trees and shrubs. This usually includes several oaks (*Quercus geminata*, *Q. myrtifolia*, *Q. Chapmanni*) saw palmetto (*Serenoa repens*), and in some localities rosemary (*Ceratiola ericoides*). From April to September the towhee is found in abundance in such habitats. The oft-mentioned tendency, noted throughout the range of the species, to move into cut-over, second-growth areas may be attributed to the physical similarity of such habitats to those found in pioneer plant associations.

It is reasonable to suppose that such favorable habitats were abundant on the transitory island and peninsular land masses that existed during the latter portions of the Cenozoic. Under such conditions then many opportunities were presented for immigration of a segment of the mainland population.

Several other birds have distributions that lend support to the theory of insular isolation. The Florida Jay, *Aphelocoma coerulescens*, is usually held to be specifically distinct from the far western members

of its genus. Geographically far removed from its relatives, this species is best viewed as a relict form. The habitat preference of this species limits its distribution in Florida to typical scrub associations, along the coast and inland. The Florida Grasshopper Sparrow, *Ammodramus savannarum floridanus*, occurs only in the central part of the state. It has allied races in some of the islands of the West Indies, and also has an insular-type distribution in Central America. The discontinuous distribution of the southern races contrasts with the continuous distribution of the forms in the northern United States.

Several other birds, including the Pine-woods and Bachmann's Sparrows (*Aimophila aestivalis aestivalis* and *A. a. bachmanni*), Eastern and Florida Cardinals (*Richmondena cardinalis cardinalis* and *R. c. floridana*) and the Northern and Southern Crested Flycatchers (*Myiarchus crinitus crinitus* and *M. c. boreus*) show lines of junction in west Florida. It is pertinent to note that *P. e. alleni*, *canaster* and *rileyi* meet in this same area.

In other groups of animals, endemism in the Florida peninsula is well recorded. Hobbs (1942: 12) lists 17 species of freshwater crayfishes (Cambarinae) which he considers as endemic forms. Six of these he believes are relicts. Carr (1940: 6) states that 11 amphibians and reptiles of Florida may be either relict or isolated species. Byers (1930: 289) concludes that the initial Florida Odonata fauna was a Nearctic one, isolated by a sea barrier. According to Berner (1950: 24), there is no necessity to hypothesize that Pleistocene islands existed in Florida so far as the Ephemeroptera are concerned. He adds, however, that there is no evidence to the contrary in the distribution of these forms today.

Professor H. K. Wallace, of the University of Florida, tells me that there is considerable evidence in the wolf spiders (*Geolycosa*) of such insular isolation. Professor H. B. Sherman, of the same institution, has called to my attention the interesting disjunctive distribution of the brown bat, *Eptesicus fuscus*, which has an endemic form in south Florida (Sherman 1936: 107).

The geological history of the peninsula of Florida furnishes abundant evidence of the possibility of isolation occurring during the Pleistocene. Other animals, both vertebrate and invertebrate, apparently were trapped by fluctuating sea levels. Some of these forms, moreover, have never since been able to rejoin the continental stocks from which they were derived, and remain as relict forms within the present peninsula.

Adams (1902) concludes that the southeastern states represent a center of dispersal from which many forms expanded their ranges, after the advance of the Pleistocene ice-caps. Variation in the eastern races of *P. erythrophthalmus* supports this conclusion in many respects.

It is unfortunate that Adams did not consider peninsular Florida in his study of this problem. If his view is correct, and if a segment of this population was isolated on the islands, it appears that the present trends in geographic variation have a rational basis.

I do not feel, on the basis of the evidence at hand, that it is possible to come to any definite conclusion concerning this problem, as it is reflected by this species. It does appear, however, that the greater weight of evidence is on the side of isolation and subsequent merging of populations. Further it seems reasonable to suppose that the pale-eyed Florida stock was derived from living or subsequently modified forms. It does not appear to be the remnant of a once widespread pre-Pleistocene stock.

SUMMARY

A review of the historical status of the species *Pipilo erythrophthalmus* from 1731 to the present is given.

A statistical study of geographical variation in size of body parts and color of irides is presented. A subjective analysis of variation in plumage color is presented. On the basis of these studies recognition of four geographic races within the species is possible. For each of these races there is given:

1. An analytical key to identification.
2. A synopsis of names applied in the past.
3. A description of the characters by which it may be recognized.
4. A discussion of its habits.
5. A statement of the breeding range and migratory behavior.
6. A list of specimens examined.

A detailed analysis of geographical variation in the several characters examined is presented. Non-geographic variation is described. Possible reasons for geographic variation in the species are explored and suggestions are presented in explanation of the patterns observed.

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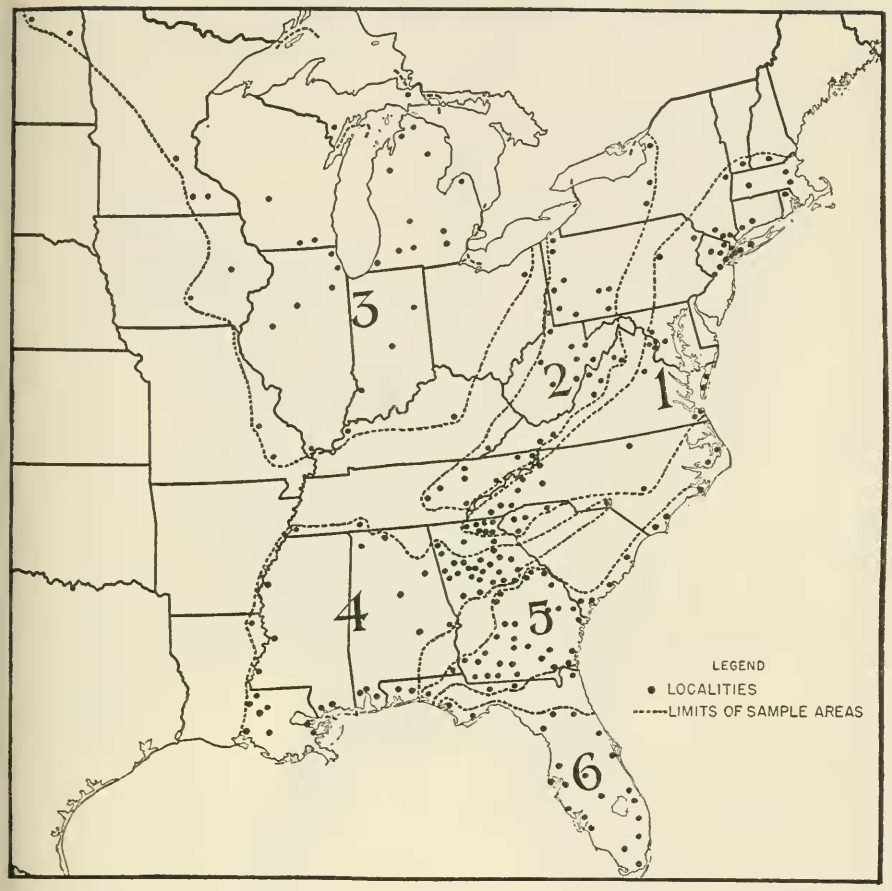
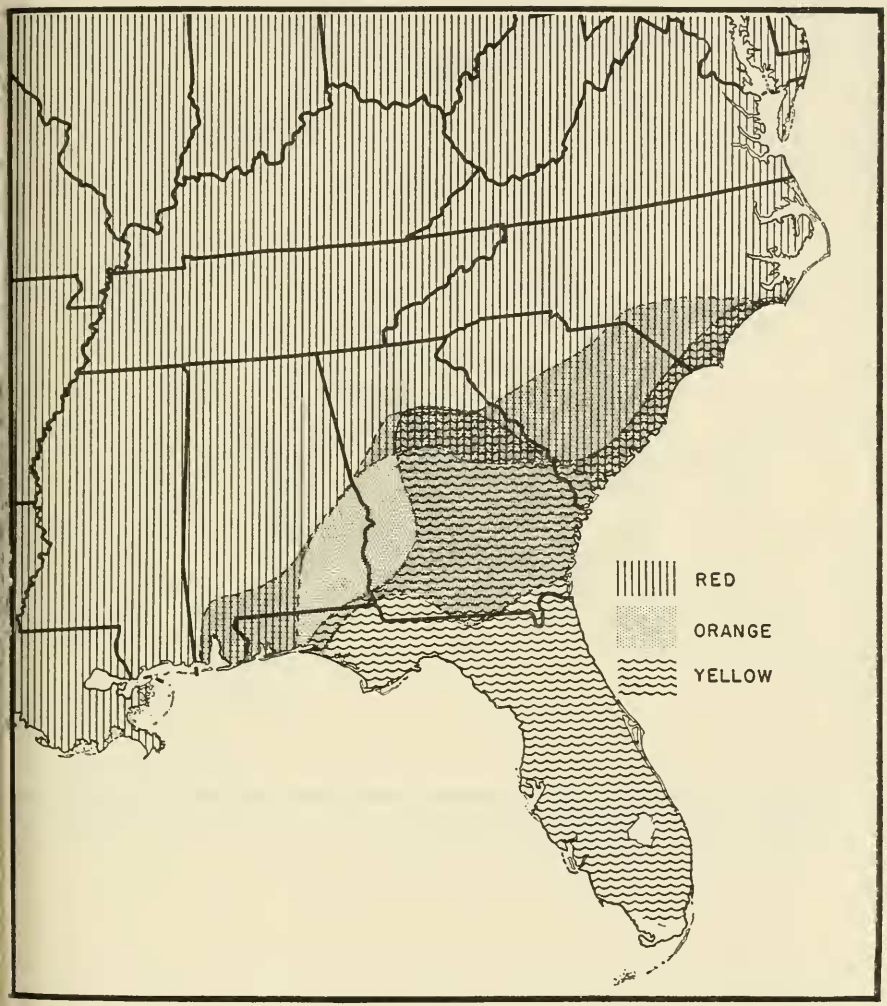
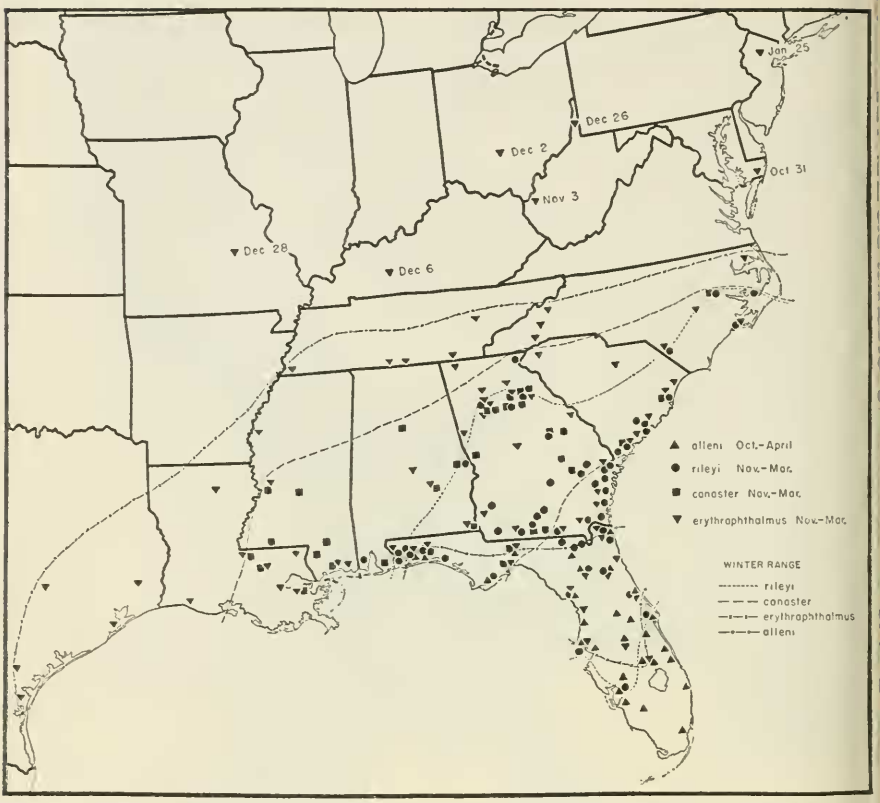


Map 1. Localities and limits of sample areas from which breeding specimens were examined. Samples 1, 2 and 3 represent *P. e. erythrophthalmus*; 4, represents *P. e. canaster*; 5, represents *P. e. rileyi* and 6, represents *P. e. alleni.*

Map 2. Breeding ranges of the subspecies of *Pipilo erythrophthalmus*.



Map 3. Geographic variation in iris color in the southeastern United States.



Map 4. Winter ranges. Note that *erythrophthalmus* and *rileyi* move farther south in peninsular Florida than does *canaster*.